INTRODUCTION

TO

ENTOMOLOGY

BY

JOHN HENRY COMSTOCK

PROFESSOR OF ENTOMOLOGY AND GENERAL INVERTEBRATE
ZOOLOGY, EMERITUS, IN CORNELL UNIVERSITY

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TO

MY OLD STUDENTS

WHOSE YOUTHFUL ENTHUSIASM WAS A CONSTANT INSPIRATION DURING

THE LONG PERIOD OF MY SERVICE AS A TEACHER THIS EFFORT

TO CONTINUE TO AID THEM IS AFFECTIONATELY

INSCRIBED

PREFACE TO PART I

THE following pages constitute the first part of a text-book of entomology that the writer has in preparation. This first part is published in advance of the completion of the entire work in response to the request of some teachers who desire that it be available for the use of their classes.

The early publication of this part of the book will not only render it immediately available but will also afford an opportunity for the suggestion of desirable changes to be made before it is incorporated in the complete work. Such suggestions are earnestly invited by the writer.

In writing this text-book much use has been made of material published in my earlier works, notably in "An Introduction to Entomology" published in 1888 and long out of print, "A Manual for the Study of Insects," in the preparation of which I was aided by Mrs. Comstock, and in the "Wings of Insects," more recently published. The more important of the other sources from which material has been drawn are indicated in the text and in the bibliography at the end of the volume. References to the bibliography are made in the text by citing the name of the author and the year in which the paper quoted was published.

A serious obstacle to the popularization of Natural History is the technical names that it is necessary to use. In order to reduce this difficulty to a minimum the pronunciation of these names is indicated by indicating the length of the vowel that receives the primary accent.

The original figures and the copies of published figures in the first chapter were drawn by Miss Anna C. Stryke; those in the three following chapters, by Miss Ellen Edmonson. I am deeply indebted to each of these artists for the painstaking care shown in her work.

Two objects are kept constantly in mind in the preparation of the text-book of which this volume is a part: first, to aid the student in laying a firm foundation for his entomological studies; and second, to make available, so far as possible in the limited space of a handbook, a knowledge of the varied phenomena of the insect world. It is hoped that those who use this book will find delight in acquiring a more intimate acquaintance with these phenomena.

JOHN HENRY COMSTOCK.

ENTOMOLOGICAL LABORATORY
CORNELL UNIVERSITY
JUNE 1919.

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THE STRUCTURE AND METAMORPHOSIS OF INSECTS

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CHAPTER I

THE CHARACTERISTICS OF INSECTS AND OF THEIR NEAR RELATIVES

PHYLUM ARTHROPODA

The Arthropods

If an insect, a scorpion, a centipede, or a lobster be examined, the body will be found to be composed of a series of more or less similar rings or segments joined together; and some of these segments will be found to bear jointed legs (Fig. 1). All animals possessing these characteristics are classed together as the *Arthrŏpoda*, one of the chief divisions or phyla of the animal kingdom.

Fig. 1.—An arthropod.

A similar segmented form of body is found among worms; but these are distinguished from the Arthropoda by the absence of legs. It should be remembered that many animals commonly called worms, as the tomato-worm, the cabbage-worm, and others, are not true worms, but are the larvæ of insects (Fig. 2). The angle-worm is the most familiar example of a true worm.

In the case of certain arthropods the distinctive characteristics of the phylum are not evident from a cursory examination. This may be due to a very generalized condition, as perhaps is true of *Peripatus;* but in most instances it is due to a secondary modification of form, the result of adaptation to special modes of life. Thus the segmentation of the body may be

Fig. 2.—A larva of an insect.

obscured, as in spiders and in mites (Fig. 3); or the jointed appendages may be absent, as in the larvæ of flies (Fig. 4), of bees, and of many other insects. In all of these cases, however, a careful study of the structure of the animal, or of its complete life-history, or of other animals that are evidently closely allied to it removes any doubt regarding its being an arthropod.

Fig. 3.—A mite, an *arthropod in which the* segmentation of the body is obscured. The southern cattle-tick, *Boophilus annulatus.*

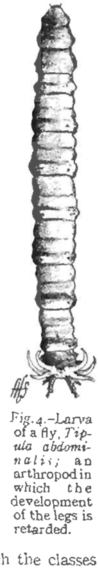

Fig. 4.—Larva of a fly, *Tipula abdominalis;* an arthropod in which the development of the legs is retarded.

The phylum Arthropoda is the largest of the phyla of the animal kingdom, including many more known species than all the other phyla taken together. This vast assemblage of animals includes forms differing widely in structure, all agreeing, however, in the possession of the essential characteristics of the Arthropoda. Several distinct types of arthropods are recognized; and those of each type are grouped together as a class.

The number of distinct classes that should be recognized, and the relation of these classes to each other are matters regarding which there are still differences of opinion; we must have much more knowledge than we now possess before we can speak with any degree of certainty regarding them.

Each of the classes enumerated below is regarded by all as a distinct group of animals; but in some cases there may be a question whether the group should be given the rank of a distinct class or not. The order in which the classes are discussed in this chapter is indicated in the following list.

LIST OF THE CLASSES OF THE ARTHROPODA

I. THE MOST PRIMITIVE ARTHROPODS
Class Onychophora, page 4

II. THE AQUATIC SERIES
Class Crustacea, page 6
Class Palæostracha, page 8

III. AN OFFSHOOT OF THE AQUATIC SERIES, SECONDARILY AERIAL
Class Arachnida, page 9

IV DEGENERATE ARTHROPODS OF DOUBTFUL POSITION

Class Pychnogonida, page 10
Class Tardigrada, page 12
Class Pentastomida, page 14

V. THE PRIMARILY AERIAL SERIES

Class Onychophora (See above).
Class Diplopoda, page 15
Class Pauropoda, page 18
Class Chilopoda, page 20
Class Symphyla, page 23
Class Myrientomata, page 24
Class Hexapoda, page 26

TABLE OF CLASSES OF THE ARTHROPODA

A. Worm-like animals, with an unsegmented body, but with many, unjointed legs . . . . ONYCHOPHORA

AA. Body more or less distinctly segmented except in a few degenerate forms.

B. With two pairs of antennæ and at least five pairs of legs; respiration aquatic . . . . CRUSTACEA

BB. Without or apparently without antennæ.

C. With well-developed aquatic respiratory organs. PALÆOSTRACHA

CC. With well-developed aerial respiratory organs or without distinct respiratory organs.

D. With well-developed aerial respiratory organs.

E. Body not resembling that of the Thysanura in form. ARACHNIDA

EE. Body resembling that of the Thysanura in form (Family Eosentomidæ) . . . . MYRIENTOMATA

DD. Without distinct respiratory organs.

E. With distinctly segmented legs.

F. Body resembling that of the Thysanura in form, but without antennæ, and with three pairs of thoracic legs and three pairs of vestigial abdominal legs (Family Acerentomidæ) . . . . MYRIENTOMATA

FF With four or five pairs of ambulatory legs; abdomen vestigial . . . . PYCHNOGONIDA

EE. Legs not distinctly segmented.

F. With four pairs of legs in the adult instar. TARDIGRADA

FF. Larva with two pairs of legs, adult without legs........................PENTASTOMIDA

BBB. With one pair, and only one, of feeler-like antennæ. Respiration aerial.

C. With more than three pairs of legs, and without wings.

D. With two pairs of legs on some of the body-segments. DIPLOPODA

DD. With only one pair of legs on each segment of the body.

E. Antennæ branched..................PAUROPODA

EE. Antennæ not branched.

F. Head without a Y-shaped epicranial suture. Tarsi of legs with a single claw each. Opening of the reproductive organs near the caudal end of the body..........................CHILOPODA

FF. Head with a Y-shaped epicranial suture, as in insects. Tarsi of legs with two claws each. Opening of the reproductive organs near the head. ....SYMPHYLA

CC. With only three pairs of legs, and usually with wings in the adult state ....HEXAPODA

CLASS ONYCHOPHORA

The genus Peripatus of authors

The members of this class are air-breathing animals, with a nearly cylindrical, unsegmented body, which is furnished with many pairs of unjointed legs. The reproductive organs open near the hind end of the body.

The class Onychŏphora occupies the position of a connecting link between the Arthropoda and the phylum Annulata or worms; and is therefore of the highest interest to students of systematic zoology. All known members of this class have been included until recently in a single genus *Perĭpatus;* but now the fifty or more known species are distributed among nearly a dozen genera.

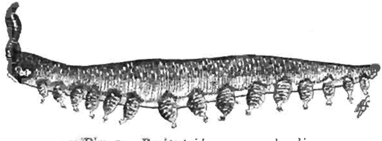

Fig. 5.—*Peripatoides novæ-zealandicæ.*

The body (Fig. 5) is nearly cylindrical, caterpillar-like in form, but is unsegmented externally. It is furnished with many pairs of legs, the number of which varies in different species. The legs have a ringed appearance, but are not distinctly jointed.

The head bears a pair of ringed antennæ (Fig. 6); behind these on
e sides of the head, there is a pair of short appendages termed oral
apillæ. The mouth opening is surrounded by a row of lobes which
onstitute the lips, and between these in the anterior part of the
outh-cavity there is an obtuse pro-
ection, which bears a row of chitinous
oints. Within the mouth cavity there
re two pairs of hooked plates, which
ave been termed the mandibles, the
wo plates of each side being regarded
s a single mandible.

Although the body is unsegmented
xternally, internally there are evi-
ences of a metameric arrangement of
arts. The ventral nerve cords, which
t first sight appear to be without
anglia, are enlarged opposite each
air of legs, and these enlargments
re regarded as rudimentary ganglia.
Ve can, therefore speak of each sec-
on of a body corresponding to a
air of appendages as a segment. The
etameric condition is farther indicated by the fact that most of
ese segments contain each a pair of nephridia; each nephridium
pening at the base of a leg.

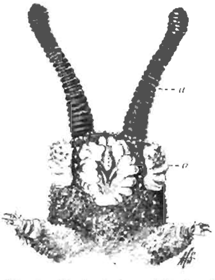

Fig. 6.—Ventral view of the head and first pair of legs of *Peripatoides*; *a*, antenna; *o*, oral papilla.

The respiratory organs are short tracheæ, which are rarely
ranched, and in which the tænidia appear to be rudimentary.* In
ome species, the spiracles are distributed irregularly; in others, they
re in longitudinal rows.

The sexes are distinct. The reproductive organs open near the
nd end of the body, either between the last or the next to the last
air of legs.

The various species are found in damp situations, under the bark
f rotten stumps, under stones or other objects on the ground. They
ave been found in Africa, in Australia, in South America, and in the
Vest Indies.

Their relationship to the Arthropoda is shown by the presence of
aired appendages, one, or perhaps two, pairs of which are modified as
ws; the presence of tracheæ which are found nowhere else except

*It is quite possible that the "short tracheæ" described by writers on the
ucture of these animals are tracheoles. See the account of the distinguishing
atures of tracheæ and tracheoles in Chapter III.

in the Arthropoda; the presence of paired ostia in the wall of the heart; and the presence of a vascular body cavity and pericardium.

They resemble the Annulata in having a pair of nephridia in most of the segments of the body corresponding to the pairs of legs, and in having cilia in the generative tracts.

An extended monograph of the Onychophora was published by Bouvier ('05–'07).

Class CRUSTACEA

The Crustaceans

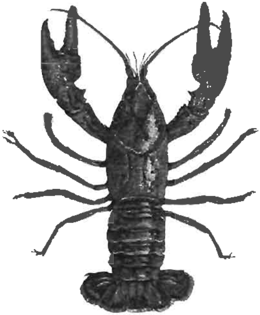

Fig. 7.—A cray-fish.

The members of this class are aquatic arthropods, which breathe by true gills. They have two pairs of antennæ and at least five pairs of legs. The position of the openings of the reproductive organs varies greatly; but as a rule they are situated far forward.

The most familiar examples of the Crustācea are the cray-fishes, the lobsters, the shrimps, and the crabs. Cray-fishes (Fig. 7) abound in our brooks, and are often improperly called crabs. The lobsters, the shrimps, and the true crabs live in salt water.

Excepting *Lĭmulus*, the sole living representative of the class described next, the Crustacea are distinguished from all other arthropods by their mode of respiration, being the only ones that breathe by true gills. Many insects live in water and are furnished with gill-like organs; but these are either tracheal gills or blood-gills, organs which differ essentially in structure from true gills, as

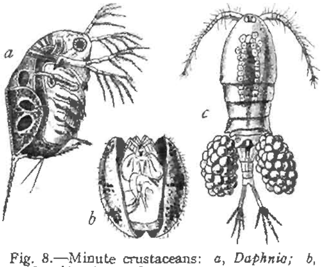

Fig. 8.—Minute crustaceans: *a*, *Daphnia*; *b*, *Cypridopsis*; *c*, *Cyclops*.

described later. The Crustacea also differ from other Arthropoda in having two pairs of antennæ. Rudiments of two pairs of antennæ have been observed in the embryos of many other arthropods; but in these cases one or the other of the two pairs of antennæ fail to develop.

The examples of crustaceans named above are the more conspicuous members of the class; but many other smaller forms abound both in the sea and in fresh water. Some of the more minute fresh-water forms are almost sure to occur in any fresh-water aquarium. In Figure 8 are represented three of these greatly enlarged. The minute crustaceans form an important element in the food of fishes.

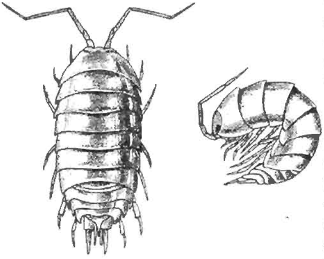

Fig. 9.—A sow-bug, *Cylisticus convexus* (From Richardson after Sars).

Some crustaceans live in damp places on land, and are often found by collectors of insects; those most often observed are the sow-bugs (Oniscoida), which frequently occur about water-soaked wood. Figure 9 represents one of these.

As there are several, most excellent text books devoted to the Crustacea, it is unnecessary to discuss farther this class in this place.

Class PALÆOSTRACHA

The King-crabs or Horseshoe-crabs

The members of this class are aquatic arthropods, which resemble the Crustacea in that they breathe by true gills, but in other respects are closely allied to the Arachnida. They are apparently without antennæ, the appendages homologous to antennæ being not feeler-like. The reproductive organs open near the base of the abdomen.

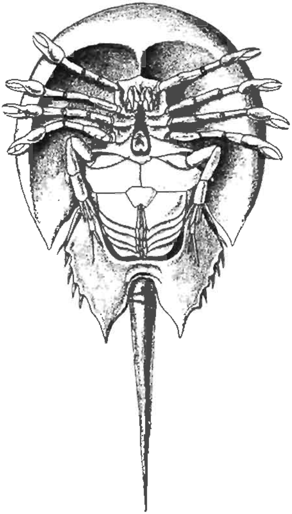

Fig. 10.—A horseshoe crab, *Limulus* (After Packard).

The class Palæŏstracha is composed almost entirely of extinct forms, there being living representatives of only a single order, the Xiphosūra, and this order is nearly extinct; for of it there remains only the genus *Lĭmulus*, represented by only five known species.

The members of this genus are known as king-crabs or horseshoe-crabs; the former name is suggested by the great size of some of the species; the latter, by the shape of the cephalothorax (Fig. 10).

The king-crabs are marine; they are found on our Atlantic Coast from Maine to Florida, in the West Indies, and on the eastern shores of Asia. They are found in from two to six fathoms of water on sandy and muddy shores; they burrow a short distance in the sand or mud and feed chiefly on worms. The single species of our coast is *Lĭmulus polyphēmus*.

Class ARACHNIDA

Scorpions, Harvestmen, Spiders, Mites, and others

The members of this class are air-breathing arthropods, in which the head and thorax are usually grown together, forming a cephalothorax, which have four pairs of legs, and which apparently have no antennæ. The reproductive organs open near the base of the abdomen.

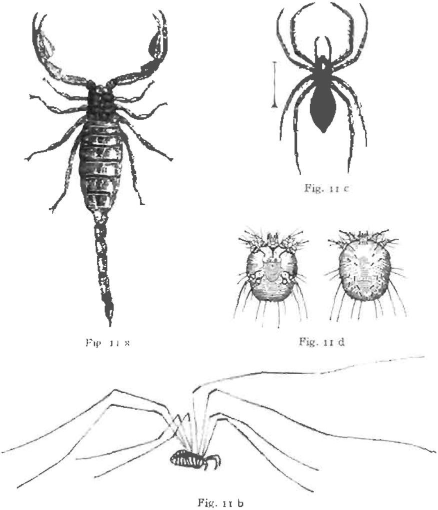

Fig. 11 a Fig. 11 c Fig. 11 d Fig. 11 b

Fig. 11.—Arachnids: *a*, a scorpion; *b*, a harvestman. *c*, a spider; *d*, an itch-mite, from below and from above.

The Arăchnida abound wherever insects occur, and are often mistaken for insects. But they can be easily distinguished by the characters given above, even in those cases where an exception occurs to some one of them. The more important of the exceptions are the following: in one order, the Solpugida, the head is distinct from the

thorax; as a rule the young of mites have only six legs, but a fourth pair is added during growth; and in the gall-mites there are only four legs.

The Arachnida are air-breathing; but it is believed that they have been evolved from aquatic progenitors. Two forms of respiratory organs exist in this class: first, book-lungs; and second, tubular tracheæ. Some members of it possess only one of these types; but the greater number of spiders possess both.

A striking characteristic of the Arachnida, which, however, is also possessed by the Palæostracha, is the absence of true jaws. In other arthropods one or more pairs of appendages are jaw-like in form and are used exclusively as jaws; but in the Arachnida the prey is crushed either by the modified antennæ alone or by these organs and other more or less leg-like appendages. The arachnids suck the blood of their victims by means of a sucking stomach; they crush their prey, but do not masticate it so as to swallow the solid parts.

In the Arachnida there exist only simple eyes.

The reproductive organs open near the base of the abdomen on the ventral side. In this respect the Arachnida resemble *Limulus*, the millipedes, and the Crustacea, and differ from the centipedes and insects.

Among the more familiar representatives of this class are the scorpions (Fig. 11, *a*), the harvestmen (Fig. 11, *b*), the spiders (Fig. 11, *c*), and the mites (Fig. 11, *d*).

As the writer has devoted a separate volume (Comstock, '12) to the Arachnida, it will not be discussed farther in this place.

Class PYCNOGONIDA

The Pycnogonids

The members of this class are marine arachnid-like arthropods, in which the cephalothorax bears typically seven pairs of jointed appendages, but in a few forms there are eight pairs, and in some the anterior two or three pairs are absent; and in which the abdomen is reduced to a legless, unsegmented condition. They possess a circulatory system, but no evident respiratory organs. The reproductive organs open through the second segment of the legs; the number of legs bearing these opening varies from one to five pairs.

The Pycnogŏnida or pycnŏgonids are marine animals, which bear a superficial resemblance to spiders (Fig. 12). Some of them are found under stones, near the low water line, on sea shores; but they

are more abundant in deep water. Some are found attached to sea-anemones, upon which they probably prey; others are found climbing

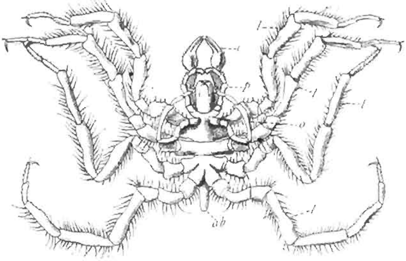

Fig. 12.—A pycnogonid, *Nymphon hispidum*: *c*, chelophore; *p*, palpus; *o*, ovigerous legs; *l*, *l*, *l*, *l*, ambulatory legs; *ab*, abdomen (After Hoeck).

over sea-weeds and Hydroids; and sometimes they are dredged in great numbers from deep water.

They possess a suctorial proboscis. In none of the appendages are the basal segments modified into organs for crushing the prey.

The cephalothorax comprises almost the entire body; the abdomen being reduced to a mere vestige, without appendages, and with no external indication of segmentation. But the presence of two pairs of abdominal ganglia indicates that originally the abdomen consisted of more than one segment.

There are typically seven pairs of appendages; but a few forms possess eight pairs; and in some the first two or three pairs are absent. The appendages, when all are present, consist of a pair of *chelophores*, each of which when well-developed consists of one or two basal segments and a chelate "hand;" the *palpi*, which are supposed to be tactile, and which have from five to ten joints when well-developed; the *ovigerous legs*, which are so-called because in the males they are used for holding the mass of eggs beneath the body; and the *ambulatory legs*, of which there are usually four pairs, but a few forms possess a fifth pair. The ambulatory legs consist each of eight segments and a terminal claw.

The only organs of special sense that have been found in these animals are the eyes. These are absent or at least very poorly

developed in some forms, especially those that are found in very deep water, *i. e.* below four or five hundred fathoms. When well-developed they are simple, and consist of two pairs, situated on a tubercle, on the head or the first compound segment of the body, the segment that bears the first four pairs of appendages.

The reproductive organs open in the second segment of the legs. In some these openings occur only in the last pair of legs; in others, in all of the ambulatory legs.

Very little is known regarding the habits of these animals. The most interesting features that have been observed is perhaps the fact that the males carry the eggs in a mass, held beneath the body by the third pair of appendages, the ovigerous legs, and also carry the young for a time.

As to the systematic position of the class Pycnogonida, very little can be said. These animals are doubtless arthropods, and they are commonly placed near the Arachnida.

Class TARDIGRADA

The Tardigrades or Bear Animalcules

The members of this class are very minute segmented animals, with four pairs of legs, but without antennæ or mouth-appendages, and without special circulatory or respiratory organs; the reproductive organs open into the intestine.

The Tardigrāda or tărdigrades are microscopic animals, measuring from one seventy-fifth to one twenty-fifth of an inch in length. They are somewhat mite-like in appearance; but are very different from mites in structure (Fig. 13 and 14).

The head bears neither antennæ nor mouth-appendages. The four pairs of legs are short, unjointed, and are distributed along the entire length of the body, the fourth pair being at the caudal end. Each leg is terminated by claws, which differ in number and form in different genera.

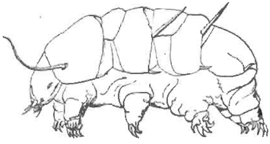

Fig. 13.—A tardigrade (After Doyère).

The more striking features of the internal structure of these animals is the absence of special circulatory and respiratory organs; the presence of a pair of chitinous teeth, either in the oral cavity or a short distance back of

ı; the presence of Malpighian tubules; the unpaired condition of he reproductive organs of both sexes; and the fact that these organs ›pen into the intestine. The central nervous system consists of a ›rain, a subœsophageal ganglion, and a ventral chain of four ganglia, ·onnected by widely separated connectives.

The tardigrades are very abundant, and are very widely disributed. Some live in fresh water, a few are marine, but most of hem live in damp places, and especially on the roots of moss, growing n gutters, on roofs or trees, or in ditches. 3ut although they are common, their ninute size and retiring habits result in heir being rarely seen except by those vho are seeking them.

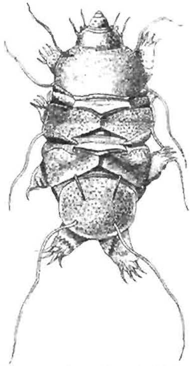
Fig. 14.—A tardigrade (After Doyère).

Many of them have the power of vithstanding desiccation for a long period. This has been demonstrated artificially by ›lacing them on a microscopic slide and illowing the mositure to evaporate slowly. The body shrinks, its skin oecomes wrinkled, and finally it assumes he appearance of a grain of sand in vhich no parts can be distinguished. In his state they can remain, it is said, for ·ears; after which, if water be added, he body swells, assumes its normal form, ınd after a time, the creatures resume heir activities.

Regarding the systematic position of his class of animals nothing definite can ›e stated beyond the fact that they are doubtless arthropods. Their elationship to the other classes of arthropods has been masked by legenerative modifications. They are placed here near the end of he series of classes of arthropods, merely as a matter of convenience, n what may be termed an appendix to the arthropod series, which ncludes animals of doubtful relationships.

Class PENTASTOMIDA

The Pentastomids or Linguatulids

The members of this class are degenerate, worm-like, parasitic arthropods, which in the adult state have no appendages, except two pairs of hooks near the mouth; the larvæ have two pairs of short legs. These animals possess neither circulatory nor respiratory organs. The reproductive organs of the male open a short distance behind the mouth; those of the female near the caudal end of the body.

The Pentastŏmida or pentăstomids are worm-like creatures, whose form has been greatly modified by their parasitic life. The adults bear little resemblance to any other arthropods. Representatives of three genera are known. These are *Linguătula* in which the body is fluke-like in form (Fig. 15) and superficially annulated; *Porocĕphalus*, in which the body is cylindrical (Fig. 16) and ringed; and *Reighărdia*, which is devoid of annulations, and with poorly developed hooks and a mouth-armature.

The arthropodan nature of these animals is indicated by the form of the larvæ, which although greatly degenerate, are less so than the adults, having two pairs of legs (Fig. 17).

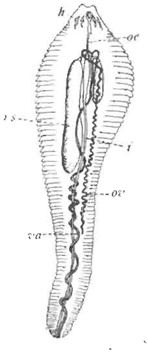

Fig. 15.—A pentastomid, *Linguatula tænioides*, female at the time of copulation: *h*, hooks; *oe*, œsophagus, *rs*, receptacula seminis, one of which is still empty; *i*, intestine; *ov*, ovary; *va*, vagina (From Lang after Leuckart).

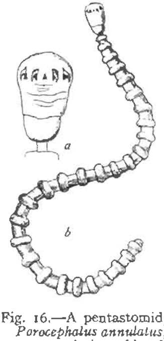

Fig. 16.—A pentastomid, *Porocephalus annulatus*; *a*, ventral view of head, greatly enlarged; *b*, ventral view of animal, slightly enlarged (After Shipley).

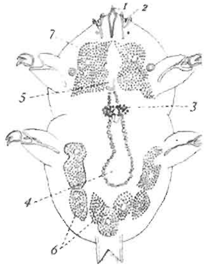

Fig. 17.—A pentastomid, larva *Porocephalus proboscideus*, s from below, highly magnified: boring anterior end; 2, first r of chitinous processes seen tween the forks of the second p 3, ventral nerve ganglion; 4. mentary canal, 5, mouth; 6. 7, gland cells (From Shipley a Stiles).

Like many of the parasitic worms, these animals, in some cases at least, pass their larval life in one host, and complete their development in another of a different species; some larvæ being found in the bodies of herbivorous animals and the adults in predacious animals that feed on these herbivorous hosts.

The systematic position of the pentastomids is very uncertain. They have been considered by some writers to be allied to the mites. But it seems better to merely place them in this appendix to the arthropod series until more is known of their relationships.

Class DIPLOPODA

The Millipedes or Diplopods

The members of this class are air-breathing arthropods in which the head is distinct, and the remaining segments of the body form a continuous region. The greater number of the body-segments are so grouped that each apparent segment bears two pairs of legs. The antennæ are short and very similar to the legs. The openings of the reproductive organs are paired, and situated behind the second pair of legs.

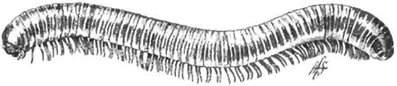

Fig. 18.—A millipede, *Spirobolus marginatus*.

The Diplŏpoda and the three following classes were formerly grouped together as a single class, the *Myriăpoda*. But this grouping has been abandoned, because it has been found that the Chilopoda are more closely allied to the insects than they are to the Diplopoda; and the Pauropoda and Symphyla are both very distinct from the Diplopoda on the one hand and the Chilopòda on the other. Owing to the very general and long continued use of the term Myriapoda, the student who wishes to look up the literature on these four classes should consult the references under this older name.

The most distinctive feature of the millipedes is that which suggested the name Diplopoda for the class, the fact that throughout the greater part of the length of the body there appears to be two pairs of legs borne by each segment (Fig. 18).

This apparent doubling of the appendages is due to a grouping of the segments in pairs and either a consolidation of the two terga of

each pair or the non-development of one of them; which of thc alternatives is the case has not been definitely determined.

It is clear, however, that there has been a grouping of the sc ments in pairs in the region where the appendages are doubled, f corresponding with each tergum there are two sterna and two pairs spiracles.

A few of the anterior body segments, usually three or four number, and sometimes one or two of the caudal segments rema single. Frequently one of the anterior single segments is legless, b the particular segment that lacks legs differs in the different famili·

The head, which is as distinct as is the head of insects, bears t antennæ, the eyes, and the mouth-parts. The antennæ are sho and usually consist each of seven segments. The eyes are usua represented by a group of ocelli on each side of the head; but the ocelli vary greatly in number, and are sometimes absent. The mouth-parts consist of an upper lip or *labrum;* a pair of *mandibles;* and a pair of jaws, which are united at the base, forming a large plate, which is known as the *gnathŏchilārium.* In the genus *Polyxenus* there is a pair of jaws between the mandibles and the gnathochilarium, which have been named the *maxĭllulæ.*

Fig. 19.—A man ble of *Julus;* cardo; *d, d,* tee *m,* muscle; *ɀ*, mala; *p,* pec nate plate; stipes (Af Latzel).

The labrum is merely the anterior part of the upper wall of the head and, as in insects, is not an appendage. The mandibles, in the forms in which they are best developed, are fitted for biting, and consist of several parts (Fig. 19); but in some forms they are vestigial. The gnathochilarium (Fig. 20) is complicated in structure, the details of which vary greatly in differe genera.

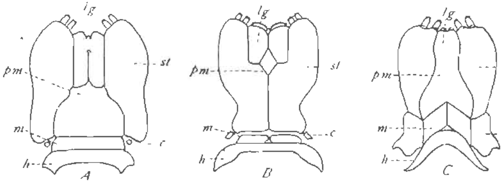

Fig. 20.—The gnathochilarium or second jaws of three diplopods; A, *Spirostr tus;* B, *Julus;* C, *Glomeris;* *c,* cardo; *h,* hypostoma; *lg,* linguæ; *m,* mentu *pm,* promentum; *st,* stipes (After Silvestri).

In one subdivision of the class Diplopoda, which is represented by the genus *Polyxenus* and a few others, the mandibles are one-jointed; and between the mandibles and the gnathochilarium there is a pair of one-jointed jaws, which have not been found in other diplopods; these are the maxillulæ (Fig. 21). The correspondence of the parts of the gnathochilarium of *Polyxenus* and its allies with the parts of the gnathocillarium of other diplopods has not been satisfactorily determined.

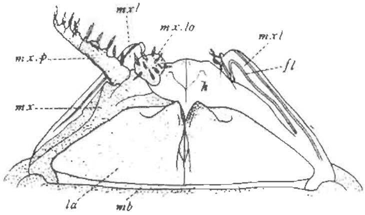

Fig. 21.—The second pair of jaws, maxillulæ, and the third pair of jaws, maxillæ or gnathochilarium, of *Polyxenus;* the parts of the maxillæ or gnathochilarium are stippled and some are omitted on the right side of the figure: *mb*, basal membrane of the labium; *la*, "labium" of Carpenter, perhaps the mentum and promentum of the gnathochilarium; *mx*, basal segment of the maxilla, perhaps the stipes of the gnathochilarium; *mx. lo*, lobe of the maxilla; *mx. p*, maxillary palpus; *h*, tongue or hypopharynx; *mxl*, maxillula; *fl*. flagellate process (After Carpenter).

Most of our more common millipedes possess stink-glands, which open by pores on a greater or less number of the body segments. These glands are the only means of defence possessed by millipedes, except the hard cuticula protecting the body.

The millipedes as a rule are harmless, living in damp places and feeding on decaying vegetable matter; but there are a few species that occasionally feed upon growing plants.

For a more detailed account of the Diplopoda see Pocock ('11).

Class PAUROPODA

The Pauropods

The members of this class are small arthropods in which the head is distinct, and the segments of the body form a single continuous region. Most of the body-segments bear each a single pair of legs. Although most of the terga of the body-segments are usually fused in couples, the legs are not grouped in double pairs as in the Diplopoda. The antennæ are branched. The reproductive organs open in the third segment back of the head.

The Paurŏpoda or pauropods are minute creatures, the described species measuring only about one twenty-fifth inch in length, more or less. They resemble centipedes in the elongated form of the body and in the fact that the legs are not grouped in double pairs as in the Diplopoda, although the terga of the body-region are usually fused in couples. These characteristics are well-shown by the dorsal and ventral views of *Pauropus* (Fig. 22 and 23).

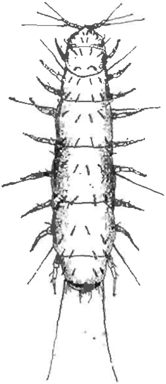

Fig. 22.—A pauropod, *Pauropus huxleyi*, dorsal aspect (After Kenyon).

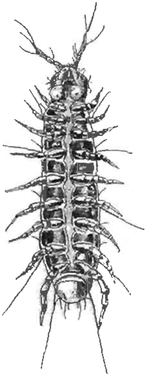

Fig. 23.—*Pauropus huxleyi*, ventral aspect (After Lubbock).

Although the pauropods resemble the chilopods in the distribution of their legs, they differ widely in the position of the openings of the reproductive organs. These open in the third segment back of the head; that of the female is single, those of the male are double.

The head is distinct from the body-region. It bears one pair of antennæ and two pairs of jaws; the eyes are absent but there is an eye-like spot on each side of the head (Fig. 24). The first pair of jaws are large, one-jointed mandibles; the second pair are short pear-shaped organs. Between these two pairs

of jaws, there is a horny framework forming a kind of lower lip to the mouth (Fig. 25). The homologies of the mouth-parts with those of the allied classes of arthropods have not been determined.

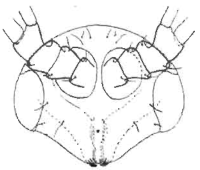

Fig. 24.—*Eurypauropus spinosus;* face showing the base of the antennæ, the mandibles, and the eye-like spots (After Kenyon).

The body-region consists of twelve segments. This is most clearly seen by an examination of the ventral aspect of the body. When the body is viewed from above the number of segments appears to be less, owing to the fact that the terga of the first ten segments are fused in couples. Nine of the body-segments bear well-developed legs. The appendages of the first segment are vestigial, and the last two segments bear no appendages.

The most distinctive feature of members of this class is the form of the antennæ, which differ from those of all other arthropods in structure. Each antenna (Fig. 26) consists of four short basal segments and a pair of one-jointed branches borne by the fourth segment. One of these branches bears a long, many-ringed filament with a rounded apical knob; and the other branch bears two such filaments with a globular or pear-shaped body between them. This is probably an organ of special sense.

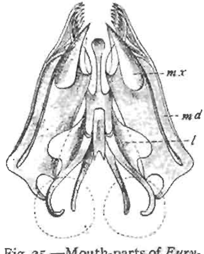

Fig. 25.—Mouth-parts of *Eurypauropus ornatus; md*, mandible; *mx*, second jaws; *l*, lower lip (After Latzel).

The pauropods live under leaves and stones and in other damp situations. Representatives of two quite distinct families are found in this country and in various other parts of the world. In addition to these a third family, the *Brachypauropŏdidæ*, is found in Europe. In this family the pairs of terga consist each of two distinct plates. Our two families are the following:

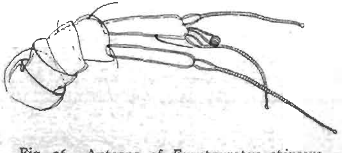

Fig. 26.—Antenna of *Eurypauropus spinosus* (After Kenyon).

Family Pauropŏdidæ.—In members of this family the head is not covered by the first tergal plate and the anal segment is not covered by the sixth tergal plate.

The best known representatives of this family belong to the genus *Pauropus* (Fig. 22). This genus is widely distributed, representatives having been found in Europe and in both North and South America. They are active, measure about one twenty-fifth inch in length, and are white.

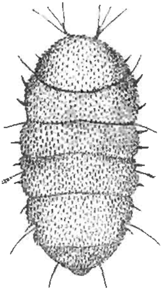

Fig. 27.—*Eurypauropus spinosus* (After Kenyon).

Family Eurypaurŏpidæ.—The members of this family are characterized by the wide form of the body, which bears some resemblance to that of a sow-bug. The head is concealed by the first tergum of the body-region; and the anal segment, by the penultimate tergum. Our most familiar representative is *Eurypauropus spinosus* (Fig. 27). This, unlike *Pauropus*, is slow in its movements.

Class CHILOPODA

The Centipedes or Chilopods

The members of this class are air-breathing arthropods in which the head is distinct, and the remaining segments of the body form a continuous region. The numerous pairs of legs are not grouped in double pairs, as in the Diplopoda. The antennæ are long and many-jointed. The appendages of the first body-segment are jaw-like and function as organs of offense, the poison-jaws. The opening of the reproductive organs is in the next to the last segment of the body.

The animals constituting the class Chilŏpoda or chīlopods are commonly known as centipedes. They vary to a considerable degree in the form of the body, but in all except perhaps the sub-class Notostigma the body-segments are distinct, not grouped in couples as in the diplopods (Fig. 28). They are sharply distinguished from the three preceding classes in the possession of poison-jaws and in having the opening of the reproductive organs at the caudal end of the body

The antennæ are large, flexible, and consist of fourteen or more segments. There are four pairs of jaws including the jaw-like

appendages of the first body-segment. These are the *mandibles* (Fig. 29, A), which are stout and consist each of two segments; the *maxillæ* (Fig. 29, B, *a*), which are foliaceous, and usually regarded as biramous; the *second maxillæ* or *palpognaths*, which are leg-like in form, consisting of five or six segments, and usually have the coxæ united on the middle line of the body (Fig. 29, B, *b*), and the *poison-claws* or *toxicognaths*, which are the appendages of the first body-segment (Fig. 29, C).

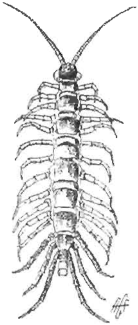

Fig. 28.—A centipede, *Bothropolys multidentatus*.

The poison-claws consist each of six segments, of which the basal one, or coxa is usually fused with its fellow, the two forming a large coxal plate, and the distal one is a strong piercing fang in which there is the opening of the duct leading from a poison gland, which is in the appendage.

The legs consist typically of six segments, of which the last, the tarsus, is armed with a single terminal claw. The last pair of legs are directed backwards, and are often greatly modified in form.

The class Chilopoda includes two quite distinct groups of animals which are regarded by Pocock ('11) as sub-classes, the Pleurostigma and the Notostigma. The names of the sub-classes refer to the position of the spiracles.

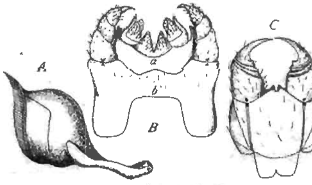

Fig. 29.—Mouth-parts of a centipede, *Geophilus flavidus*. A, right mandible, greatly enlarged. B, the two pairs of maxillæ, less enlarged; *a*, the united coxæ of the maxillæ; *b*, the united coxæ of the second maxillæ or palpognaths. C, the poison claws or toxicognaths (After Latzel)

SUB-CLASS PLEUROSTIGMA

The typical Centipedes

In the typical centipedes, the sub-class Pleurostigma, the spiracles are paired and are situated in the sides of the segments that bear them. Each leg-bearing segment contains a distinct tergum and sternum, the number of sterna never exceeding that of the terga. The eyes

when present are simple ocelli; but there may be a group of ocelli on each side of the head. Figure 28 represents a typical centipede.

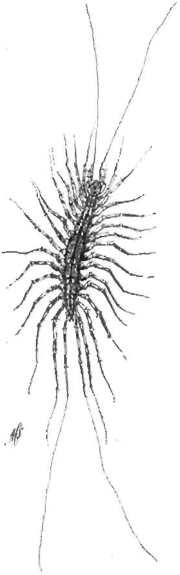

Fig. 30.—*Scutigera forceps.*

Sub-Class NOTOSTIGMA

Scutigera and its Allies

In the genus *Scutigera* and its allies, which constitute the sub-class Notostigma, there is a very distinctive type of respiratory organs. There is a single spiracle in each of the spiracle-bearing segments, which are seven in number. These spiracles open in the middle line of the back, each in the hind margin of one of the seven prominent terga of the body-region. Each spiracle leads into a short sac from which the tracheal tubes extend into the pericardial blood-sinus.

There are fifteen leg-bearing segments in the body region; but the terga of these segments are reduced to seven by fusion and suppression.

The eyes differ from those of all other members of the old group Myriapoda in being compound, the ommatidia resembling in structure the ommatidia of the compound eyes of insects.

The following species is the most familiar representative of the Notostigma.

The house centipede, *Scutigera fórceps.*—This centipede attracts attention on account of the great length of its appendages (Fig. 30), and the fact that it is often seen, in the regions where it is common, running on the walls of rooms in dwelling houses, where it hunts for flies and other insects. It prefers damp situations; in houses it is most frequently found in cellars, bathrooms, and closets. Sometimes it becomes very abundant in conservatories, living among the stored pots and about the heating pipes. It is much more common in the South than in the North.

The body of the adult measures an inch or a little more in length. It is difficult to obtain perfect specimens, as they shed their legs when seized.

Class SYMPHYLA

The Symphylids

The members of this class are small arthropods in which the head is distinct, and the segments of the body form a single continuous region. Most of the body-segments bear a single pair of legs. The antennæ are very long and many-jointed. The head bears a Y-shaped epicranial suture, as in insects. The opening of the reproductive organs is in the third segment behind the head.

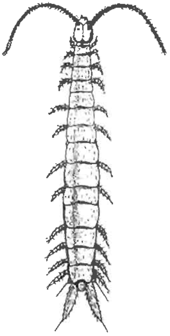

Fig. 31.—*Scolopendrella* (After Latzel).

The class Sўmphyla includes a small number of many-legged arthropods which exhibit striking affinities with insects, and especially with the Thysanura. The body is centipede-like in form (Fig 31). The head is distinct, and is not bent down as it is in the diplopods and pauropods; it is shaped as in Thysanura and bears a Y-shaped epicranial suture. The body-region bears fifteen terga, which are distinct, not grouped in couples as in the two preceding classes; and there are eleven or twelve pairs of legs.

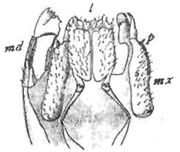

Fig. 32.— Mouth-parts of *Scolopendrella* seen from below: *md*, mandible; *mx*, maxillæ; *s*, stipes; *p*, palpus; *l*, second maxillæ or labium. The mandible on the right side of the figure is omitted (After Hansen).

The antennæ are long and vary greatly in the number of the segments. There are no eyes. Four pairs of jaws are present; these are the mandibles, the maxillulæ, the maxillæ, and the second maxillæ or labium.

The *mandibles* (Fig. 32, *md*) are two-jointed; the *maxillulæ* (Fig. 33, *m*) are small, not segmented, and are attached to a median lobe or *hypopharynx* (Fig. 33, *h*); they are hidden when the mouth-parts are viewed from below as represented in Figure 32; the *maxillæ* (Fig.

32, *mx*) resemble in a striking degree the maxillæ of insects, consisting of a long stipes, (*s*), which bears a minute palpus, (*p*), and an outer and inner lobe; the *second maxillæ* or *labium* (Fig. 32, *l*) also resembles the corresponding part of the more generalized insects, being composed of a pair of united gnathites.

Fig. 33.—The hypopharynx (h) and maxillulæ (m) of *Scolopendrella* (After Hansen).

The legs of the first pair are reduced in size and in the number of their segments. The other legs consist each of five segments; the last segment bears a pair of claws. Excepting the first two pairs of legs, each leg bears on its proximal segment a slender cylindrical process, the *parapōdium* (Fig. 34, p). These parapodia appear to correspond with the styli of the Thysanura.

Fig. 34.—A leg of *Scolopendrella*; *p*, parapodium

At the caudal end of the body there is a pair of appendages, which are believed to be homologous with the *cerci* of insects (Fig. 35, *c*).

A striking peculiarity of the symphylids is that they possess only a single pair of tracheal tubes, which open by a pair of spiracles, situated in the head beneath the insertion of the antennæ.

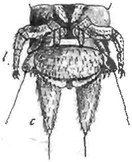

Fig. 35.—The caudal end of the body of *Scolopendrella*; *l*, leg; *c*, cercus (After Latzel).

The members of this class are of small size, the larger ones measuring about one-fourth inch in length. They live in earth under stones and decaying wood, and in other damp situations. Immature individuals possess fewer body-segments and legs than do adults.

Less than thirty species have been described; but doubtless many more remain to be discovered.

The known species are classed in two genera: *Scolopendrĕlla* and *Scutigerĕlla*. In the former the posterior angles of the terga are produced and angular; while in the latter they are rounded.

A monograph of the Symphyla has been published by Hansen ('03).

Class MYRIENTOMATA

The Myrientomatids

The members of this class are small arthropods in which the body is elongate, as in the Thysanura, fusiform, pointed behind, and depressed; it may be greatly extended and retracted. The antennæ and cerci are

absent. The oral appratus is suctoral, and consists of three pairs of gnathites. There are three pairs of thoracic legs, and three pairs of vestigial abdominal legs. The abdomen is composed of eleven segments and a telson. The opening of the reproductive organs is unpaired, and near the hind end of the body. The head bears a pair of organs, termed pseudoculi, the nature of which has not been definitely determined.

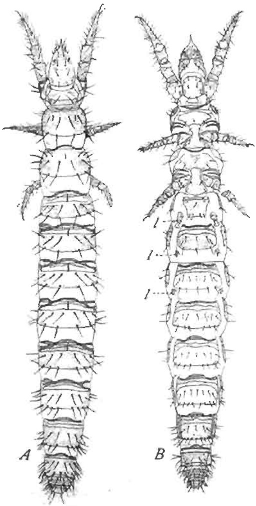

Fig. 36.—***Acerentomon doderoi:*** **A, dorsal aspect; B, ventral aspect; l, l, l, vestigial abdominal legs (After Berlese).**

The known members of this class are very small arthropods, the body measuring from one-fiftieth to three-fiftieths of an inch in length. The form of the body is shown by Figure 36.

These exceedingly interesting creatures are found in damp situations, as in the humus of gardens; as yet very little is known of their geographical distribution, as almost all of the studies of them have been made by two Italian naturalists.

The first discovered species was described in 1907 by Professor F. Silvestri of Portici, who regarded it as the type of a distinct order of insects, for which he proposed the name Protura. Later Professor Antonio Berlese of Florence described several additional species, and published an extended monograph of the order (Berlese '09 *b*).

Professor Berlese concluded that these arthropods are more closely allied to the "Myriapoda" and especially to the Pauropoda than they are to the insects, and changed the name of the order, in an arbitrary manner, to Myrientomāta.

It seems clear to me that in either case whether the order is classed among the insects or assigned to some other position it should be known by the name first given to it, that is, the Protūra

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In the present state of our knowledge of the affinities of the classes of arthropods, it seems best to regard the Protura as representing a separate class, of rank equal to that of the Pauropoda, Symphyla, etc.: and for this class I have adopted the name proposed for the group by Berlese, that is the Myrientomāta.

The class Myrientomata includes a single order.

Order PROTURA

As this is the only order of the class Myrientomata now known it must be distinguished by the characteristics of the class given above.

Two families have been established: the Acerentŏmidæ, characterized by the absence of spiracles and tracheæ; and the Eosentŏmidæ the members of which possess two pairs of thoracic spiracles and simple tracheæ.

That the Protura are widely distributed is evident from the fact that in addition to those found in Italy representatives of the order have been found in peat in Hampshire, England, and others have been taken near New York City.

Class HEXAPODA

The Insects

The members of this class are air-breathing arthropods, with distinct head, thorax, and abdomen. They have one pair of antennæ, three pairs of legs, and usually one or two pairs of wings in the adult state. The opening of the reproductive organs is near the caudal end of the body.

We have now reached in our hasty review of the classes of arthropods the class of animals to which this book is chiefly devoted, the Hexapoda,* or Insects, the study of which is termed entomology.

Insects are essentially terrestrial; and in the struggle for existence they are the most successful of all terrestrial animals, outnumbering both in species and individuals all others together. On the land they abound under the greatest variety of conditions, special forms having been evolved fitted to live in each of the various situations where other animals and plants can live; but insects are not restricted to dry land, for many aquatic forms have been developed.

The aquatic insects are almost entirely restricted to small bodies of fresh water, as streams and ponds, where they exist in great numbers. Larger bodies of fresh water and the seas are nearly destitute of them except at the shores.

*Hexăpoda: *hex* (ἕξ), six; *pous* (πούς), a foot.

As might be inferred from a consideration of the immense number of insects, the part they play in the economy of nature is an exceedingly important one. Whether this part is to be considered a beneficial or an injurious one when judged from the human standpoint would be an exceedingly difficult question to determine. For if insects were to be removed from the earth the whole face of nature would be changed.

While the removal of insects from the earth would eliminate many pests that prey on vegetation, would relieve many animals of annoying parasites, and would remove some of the most terrible diseases to which our race is subject, it would result in the destruction of many groups of animals that depend, either directly or indirectly, upon insects for food, and the destruction of many flowering plants that depend upon insects for the fertilization of their blossoms. Truly this world would speedily become a very different one if insects were exterminated.

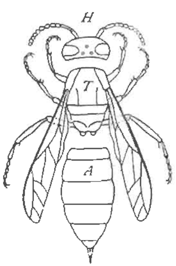

Fig. 37.—Wasp with head, thorax, and abdomen separated.

It may seem idle to consider what would be the result of the total destruction of insects; but it is not wholly so. A careful study of this question will do much to open our eyes to an appreciation of the wonderful "web of life" of which we are a part.

Most adult insects can be readily distinguished from other arthropods by the form of the body, the segments being grouped into three distinct regions, head, thorax, and abdomen (Fig. 37), by the possession of only three pairs of legs, and in most cases by the presence of wings.

The head bears a single pair of antennæ, the organs of sight, and the mouth-parts. To the thorax, are articulated the organs of locomotion, the legs and the wings when they are present. The abdomen is usually without organs of locomotion but frequently bears other appendages at the caudal end.

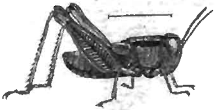
Fig. 38.—Nymph of the red-legged locust.

These characteristics are also possessed by the immature forms of several of the orders of insects; although with these the wings are

rudimentary (Fig. 38). But in other orders of insects the immature forms have been greatly modified to adapt them to special modes of life, with the result that they depart widely from the insect type. For example, the larvæ of bees, wasps, flies, and many beetles are legless and more or less worm-like in form (Fig. 4); while the larvæ of butterflies and moths possess abdominal as well as thoracic legs (Fig. 39).

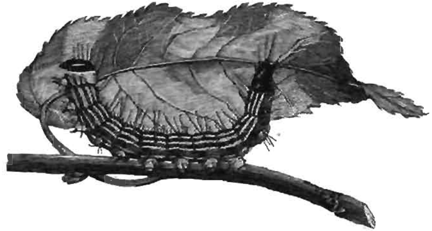

Fig. 39.—A larva of a handmaid moth, *Datana*.

Although the presence of wings in the adult state is characteristic of most insects, there are two orders of insects, the Thysanura and the Collembola, in which wings are absent. These orders represent a branch of the insect series that separated from the main stem before the evolution of wings took place; their wingless condition is, therefore, a primitive one. There are also certain other insects, as the lice and bird-lice, that are wingless. But it is believed that these have descended from winged insects, and have been degraded by their parasitic life; in these cases the wingless condition is an acquired one. Beside these there are many species belonging to orders in which most of the species are winged that have acquired a wingless condition in one or both sexes. Familiar examples of these are the females of the Coccidæ (Fig. 40), and the females of the canker-worm moths. In fact, wingless forms occur in most of the orders of winged insects.

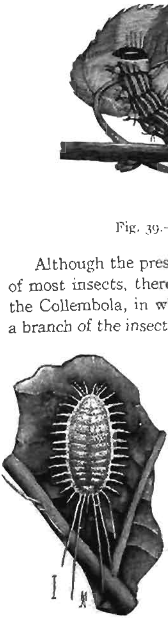

Fig. 40.—A mealy-bug, *Dactylopius*.

As the structure and transformations of insects are described in detail in the following chapters, it is unnecessary to dwell farther on the characteristics of the Hexapoda in this place.

CHAPTER II.

THE EXTERNAL ANATOMY OF INSECTS

I. THE STRUCTURE OF THE BODY-WALL

a. THE THREE LAYERS OF THE BODY-WALL

THREE, more or less distinct, layers can be recognized in the body-wall of an insect: first, the outer, protecting layer, the *cuticula;* second, an intermediate, cellular layer, the *hypodermis;* and third, an inner, delicate, membranous layer, the *basement membrane*. These layers can be distinguished only by a study of carefully prepared, microscopic sections of the body-wall. Figure 41 represents the appearance of such a section. As the outer and inner layers are derived from the hypodermis, this layer will be described first.

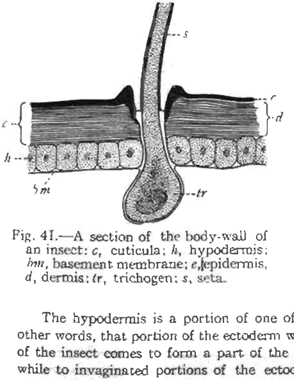

Fig. 41.—A section of the body-wall of an insect: *c*, cuticula; *h*, hypodermis; *bm*, basement membrane; *e*, epidermis, *d*, dermis; *tr*, trichogen; *s*, seta.

The hypodermis.—The active living part of the body-wall consists of a layer of cells, which is termed the *hypo-dĕrmis* (Fig. 41, *h*).

The hypodermis is a portion of one of the germ-layers, the ectoderm. In other words, that portion of the ectoderm which in the course of the development of the insect comes to form a part of the body-wall is termed the hypodermis; while to invaginated portions of the ectoderm other terms are applied, as the epithelial layer of the tracheæ, the epithelial layer of the fore-intestine, and the epithelial layer of the hind-intestine.

The cells of which the hypodermis is composed vary in shape; but they are usually columnar in form, constituting what is known to histologists as a columnar epithelium. Sometimes the cells are so flattened that they form a simple pavement epithelium. I know of no case in which the hypodermis consists of more than a single layer of cells; although in wing-buds and buds of other appendages, where the cells are fusiform, and are much crowded, it appears to be irregu-

larly stratified. This is due to the fact that the nuclei of different cells are in different levels.

The trichogens.—Certain of the hypodermal cells become highly specialized and produce hollow, hair-like organs, the setæ, with which they remain connected through pores in the cuticula. Such a hair-forming cell is termed a *trichogen* (Fig. 41, *tr*); and the pore in the cuticula is termed a *trichopore*.

The cuticula.—Outside of the hypodermis there is a firm layer, which protects the body and serves as a support for the internal organs; this is the *cuticula* (Fig. 41, *c*). The cuticula is produced by the hypodermis; the method of its production is discussed in a later chapter where the molting of insects is treated. The cuticula is not affected by caustic potash; it is easy, therefore, to separate it from the tissues of the body by boiling or soaking it in an aqueous solution of this substance.

Chitin.—The well-known firmness of the larger part of the cuticula of adult insects is due to the presence in it of a substance which is termed *chitin*. This substance bears some resemblance in its physical properties to horn; but is very different from horn in chemical composition. In thin sheets it is yellowish in color; thicker layers of it are black. It is stained yellow by picric acid and pink by safranin.

Chitinized and non-chitinized cuticula.—When freshly formed, the cuticula is flexible and elastic, and certain portions of it, as at the nodes of the body and of the appendages, remain so. But the greater part of the cuticula, especially of adult insects, usually becomes firm and inelastic; this is probably due to a chemical change resulting in the production of chitin. What the nature of this change is or how it is produced is not yet known, but it is evident that a change occurs; we may speak, therefore, of chitinized cuticula and non-chitinized cuticula. This difference is well-shown in sections of the cuticula stained by picro-carmine, which colors the chitinized portions yellow and the non-chitinized parts pink; it can be shown also by other double stains, as eosin-methylene-blue.

Chitinized cuticula is inelastic, while non-chitinized cuticula is elastic. The elasticity of non-chitinized cuticula is well-shown by the stretching of the body-wall after a molt and before the hardening of the cuticula. It is also shown by the expanding of the abdomen of females to accommodate the growing eggs, the stretching of the body-wall taking place in the non-chitinized portions between the segments. An extreme case of this is shown by the queens of Termites.

The formation of chitin is not restricted to the hypodermis, but is a property of the invaginated portions of the ectoderm; the fore-intestine, the hind-intestine, and the tracheæ are all lined with a cuticular layer, which is continuous with the cuticula of the body-wall and is chitinized. The most marked case of internal formation of chitin is the development of large and powerful teeth in the proventriculus of many insects.

The epidermis and the dermis.—Two quite distinct parts of the cuticula are recognized by recent writers; these are distinguished as the *epidermis* and the *dermis* respectively.

The epidermis is the external portion; in it are located all of the cuticular pigments; and from it are formed all scales, hairs, and other surface structures. It is designated by some writers as the *primary cuticula.* (Fig. 41, *e*).

The dermis is situated beneath the epidermis. It is formed in layers, which give sections of the cuticula the well-known laminate appearance. It is sometimes termed the *secondary cuticula* (Fig. 41,*d*)

The basement membrane.—The inner ends of the hypodermal cells are bounded by a more or less distinct membrane; this is termed the *basement membrane* (Fig. 41, *bm*). The basement membrane is most easily seen in those places where the inner ends of the hypodermal cells are much smaller than the outer ends; here it is a continuous sheet connecting the tips of the hypodermal cells.

b. THE EXTERNAL APOPHYSES OF THE CUTICULA

The outer surface of the cuticula bears a wonderful variety of projections. These, however, can be grouped under two heads: first, those that form an integral part of the cuticula; and second, those that are connected with the cuticula by a joint. Those that form an integral part of the cuticula are termed *apŏphysēs;* those that are connected by a joint are termed *appendages of the cuticula.*

The cuticular nodules.—The most frequently occurring outgrowths of the cuticula are small, more or less conical nodules. These vary greatly in size, form, and distribution over the surface of the body in different species of insects, and are frequently of taxonomic value.

The fixed hairs.—On the wings of some insects, as the Trichoptera and certain of the Lepidoptera, there is in addition to the more obvious setæ and scales many very small, hair-like structures, which

differ from setæ in being directly continuous with the cuticula, and not connected with it by a joint; these are termed the *fixed hairs*.

The mode of origin and development of the fixed hairs has not been studied; they may be merely elongated cuticular nodules.

The spines.—The term spine has been used loosely by writers on entomology. Frequently large setæ are termed spines. In this work such setæ are called spine-like setæ; and the term spine is applied only to outgrowths of the cuticula that are not separated from it by a joint. Spines differ also from spine-like setæ in being produced by undifferentiated hypodermal cells and are usually if not always of multicellular origin, while each seta is produced by a single trichogen cell. The accompanying diagram (Fig. 42) illustrates this difference.

c. THE APPENDAGES OF THE CUTICULA

Under this head are included those outgrowths of the cuticula that are connected with it by a joint. Of these there are two quite distinct types represented by the spurs and the setæ respectively.

The spurs.—There exist upon the legs of many insects appendages which on account of their form and position have been termed spurs. Spurs resemble the true spines described above and differ from setæ in being of multicellular origin; they differ from spines in being appendages, that is, in being connected with the body-wall by a joint.

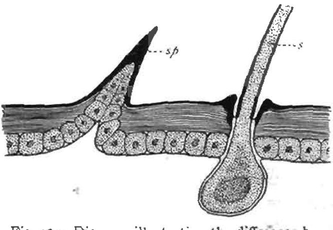

Fig. 42.—Diagram illustrating the difference between a spine (sp) and a seta (s).

The setæ.—The setæ are what are commonly called the hairs of insects. Each seta (Fig. 42, *s*) is an appendage of the body-wall, which arises from a cup-like cavity in the cuticula, the *alvëolus*, situated at the outer end of a perforation of the cuticula, the *trichopore;* and each seta is united at its base with the wall of the trichopore by a ring of thin membrane, the *articular membrane* of the seta.

The setæ are hollow; each is the product of a single hypodermal cell, a trichogen (Fig. 42), and is an extension of the epidermal

In addition to the trichogen there may be a gland-cell opening into the seta, thus forming a glandular hair, or a nerve may extend to the seta, forming a sense-hair; each of these types is discussed later.

The most common type of seta is bristle-like in form; familiar examples of this type are the hairs of many larvæ. But numerous modifications of this form exist. Frequently the setæ are stout and firm, such are the *spine-like setæ;* others are furnished with lateral prolongations, these are the *plumose hairs;* and still others are flat, wide, and comparatively short, examples of this form are the *scales* of the Lepidoptera and of many other insects.

The taxonomic value of setæ.—In many cases the form of the setæ and in others their arrangement on the cuticula afford useful characteristics for the classification of insects. Thus the scale-like form of the setæ on the wing-veins of mosquitoes serves to distinguish these insects from closely allied midges; and the clothing of scales is one of the most striking of the characteristics of the Lepidoptera.

The arrangement of the setæ upon the cuticula, in some cases at least, is a very definite one. Thus Dyar ('94) was able to work out a classification of lepidopterous larvæ by a study of the setæ with which the body is clothed.

A classification of setæ.—If only their function be considered the hairs or setæ of insects can be grouped in the three following classes:

(1) *The clothing hairs.*—Under this head are grouped those hairs and scales whose primary function appears to be merely the protection of the body or of its appendages. So far as is known, such hairs contain only a prolongation of the trichogen cell that produced them. It should be stated, however, that this group is merely a provisional one; for as yet comparatively little is known regarding the relation of these hairs to the activities of the insects possessing them.

In some cases the clothing hairs have a secondary function. Thus the highly specialized overlapping scales of the wings of Lepidoptera, which are modified setæ, may serve to strengthen the wings; and the markings of insects are due almost entirely to hairs and scales. The fringes on the wings of many insects doubtless aid in flight, and the fringes on the legs of certain aquatic insects also aid in locomotion.

(2) *The glandular hairs.*—Under this head are grouped those hairs that serve as the outlets of gland cells. They are discussed in the next chapter, under the head of hypodermal glands.

(3) *The sense-hairs*—In many case a seta, more or less modified in form, constitutes a part of a sense-organ, either of touch, taste, or smell; examples of these are discussed in the next chapter.

d. THE SEGMENTATION OF THE BODY

The cuticular layer of the body-wall, being more or less rigid, forms an external skeleton; but this skeleton is flexible along certain transverse lines, thus admitting of the movements of the body, and producing the jointed appearance characteristic of insects and of other arthropods.

An examination of a longitudinal section of the body-wall shows that it is a continuous layer and that the apparent segmentation is due to infoldings of it (Fig. 43).

Fig. 43.—Diagram of a longitudinal section of the body-wall of an insect.

The body-segments, somites, or metameres.—Each section of the body between two of the infoldings described above is termed a *body-segment*, or *sŏmīte*, or *mĕtamere*.

The transverse conjunctivæ.—The infolded portion of the body-wall connecting two segments is termed a *conjunctiva*. These conjunctivæ may be distinguished from others described later as the *transverse conjunctivæ*.

The conjunctivæ are less densely chitinized than the other portions of the cuticula; their flexibility is due to this fact, rather than to a comparative thinness as has been commonly described.

e. THE SEGMENTATION OF THE APPENDAGES

The segmentation of the legs and of certain other appendages is produced in the same way as that of the body. At each node of an appendage there is an infolded, flexible portion of the wall of the appendage, a conjunctiva, which renders possible the movements of the appendage.

f. THE DIVISIONS OF A BODY-SEGMENT

In many larvæ, the cuticula of a large part of the body-wall is of the non-chitinized type; in this case the wall of a segment may form a ring which is not divided into parts. But in most nymphs, naiads, and adult insects, there are several densely chitinized parts in the wall of each segment; this enables us to separate it into well-defined portions.

The tergum, the pleura, and the sternum.—The larger divisions of a segment that are commonly recognized are a dorsal division, the

tergum; two lateral divisions, one on each side of the body, the *pleura;* and a ventral division, the *sternum*.

Each of these divisions may include several definite areas of chitinization. In this case the sclerites of the tergum are referred to collectively as the *tergites*, those of each pleurum, as the *pleurites*, and those constituting the sternum, as the *sternites*.

The division of a segment into a tergum, two pleura, and a sternum are most easily seen in the wing-bearing segments, but it can be recognized also in the prothorax of certain generalized insects. This is especially the case in many Orthoptera, as cockroaches and walking-sticks, where the pleura of the prothorax are distinct from the tergum and the sternum. In the abdomen it is evident that correlated with the loss of the abdominal appendages a reduction of the pleura has taken place.

The lateral conjunctivæ.—On each side of each abdominal segment of adults the tergum and the sternum are united by a strip of non-chitinized cuticula; these are the lateral conjunctivæ. Like the transverse conjunctivæ, the lateral ones are more or less infolded.

The sclerites.—Each definite area of chitinization of the cuticula is termed a *sclērite*.

The sutures.—The lines of separation between the sclerites are termed *sūtures*. Sutures vary greatly in form; they may be infolded conjunctivæ; or they may be mere lines indicating the place of union between two sclerites. Frequently adjacent sclerites grow together so completely that there is no indication of the suture; in such cases the suture is said to be *obsolete*.

The median sutures.—On the middle line of the tergites and also of the sternites there frequently exist longitudinal sutures. These are termed the *median sutures*. They represent the lines of the closure of the embryo, and are not taken into account in determining the number of the sclerites.

The dorsal median suture has been well-preserved in the head and thorax, as it is the chief line of rupture of the cuticula at the time of molting.

The piliferous tubercles of larvæ.—The setæ of larvæ are usually borne on slightly elevated annular sclerites; these are termed *pilĭf-erous tubercles*.

The homologizing of the sclerites.—While it is probable that the more important sclerites of the body in winged insects have been derived from a common winged ancestor and, therefore, can be homologized, many secondary sclerites occur which can not be thus homologized.

g. THE REGIONS OF THE BODY

The segments of the body in an adult insect are grouped into three, more or less well-marked regions: the *head*, the *thorax*, and the *abdomen*. Each of these regions consists of several segments more or less closely united.

The head is the first of these regions; it bears the mouth-parts, the eyes, and the antennæ. The thorax is the second region; it bears the legs and the wings if they are present. The abdomen is the third region; it may bear appendages connected with the organs of reproduction.

II. THE HEAD

The external skeleton of the head of an insect is composed of several sclerites more or less closely united, forming a capsule, which includes a portion of the viscera, and to which are articulated certain appendages.

a. THE CORNEAS OF THE EYES

The external layer of the organs of vision, the corneas of the eyes, is, in each case, a translucent portion of the cuticula. It is a portion of the skeleton of the head, which serves not merely for the admission of light but also to support the more delicate parts of the visual apparatus.

The corneas of the compound eyes.—The compound eyes are the more commonly observed eyes of insects. They are situated one on each side of the head, and are usually conspicuous. Sometimes, as in dragon-flies, they occupy the larger part of the surface of the head.

The compound eyes are easily recognized as eyes; but when one of them is examined with a microscope it is found to present an appearance very different from that of the eyes of higher animals, its surface being divided into a large number of six-sided divisions (Fig. 44); hence the term compound eyes applied to them.

Fig. 44.—Part of a cornea of a compound eye.

A study of the internal structure of this organ has shown that each of these hexagonal divisions is the outer end of a distinct element of the eye. Each of these elements is termed an *ommatidium*. The number of ommatidia of which a compound eye is composed varies greatly; there may be not more than fifty, as in certain ants, or there may be many thousand, as in a butterfly or a dragon-fly.

As a rule, the immature stages of insects with a gradual metamorphosis and also those of insects with an incomplete metamorphosis,

that is to say nymphs and naiads possess compound eyes. But the larvæ of insects with a complete metamorphosis, except *Corethra*, do not possess well-developed compound eyes; although there are frequently a few separate ommatidia on each side of the head. These are usually termed ocelli; but the ocelli of larvæ should not be confused with the ocelli of nymphs, naiads, and adults.

The corneas of the ocelli.—In addition to the compound eyes most nymphs, naiads, and adult insects possess other eyes, which are termed *ocelli*. The cornea of each ocellus is usually a more or less nearly circular, convex area, which is not divided into facets. The typical number of ocelli is four; but this number is rarely found. The usual number is three, a median ocellus, which has been derived from a pair of ocelli united, and a distinct pair of ocelli. Frequently the median ocellus is lacking, and less frequently, all of the ocelli have been lost. The position of the ocelli is discussed later.

b. THE AREAS OF THE SURFACE OF THE HEAD

In descriptions of insects it is frequently necessary to refer to the different regions of the surface of the head. Most of these regions were named by the early insect anatomists; and others have been described by more recent writers.

This terminology is really of comparatively little morphological value; for in some cases a named area includes several sclerites, while in others only a portion of a sclerite is included. This is due to the fact that but few of the primitive sclerites of the head have remained distinct, and some of them greatly overshadow others in their development. The terms used, however, are sufficiently accurate to meet the needs of describers of species, and will doubtless continue in use. It is necessary, therefore, that students of entomology become familiar with them.

The best landmark from which to start in a study of the areas of the surface of the head is the *epicranial suture*, the inverted Y-shaped suture on the dorsal part of the head, in the more generalized insects (Fig. 45, *e. su.*). Behind the arms of this suture there is a series of *paired* sclerites, which meet on the dorsal wall of the head, the line of union being the stem of the Y, a median suture; and between the arms of the Y and the mouth there are typically three *single* sclerites (Fig. 45, F, C, L). It is with these unpaired sclerites that we will begin our definitions of the areas of the head.

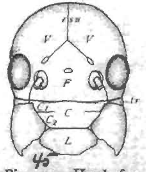

Fig. 45.—Head of a cricket.

The front.—The front is the unpaired sclerite between the arms of the epicranial suture (Fig. 45, F).

In the more generalized insects at least, if not in all, the front bears the median ocellus; and in the Plecoptera, the paired ocelli also. Frequently the suture between the front and the following sclerite, the clypeus, is obsolete; but as it ends on each side in the invagination which forms an anterior arm of the tentorium or endo-skeleton (Fig. 46, *at*), its former position can be inferred, at least in the more generalized insects, even when no other trace of it remains. In Figure 46 this is indicated by a dotted line.

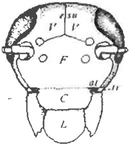

Fig. 46.—Head of a cockroach.

The clypeus.—The *clypeus* is the intermediate of the three unpaired sclerites between the epicranial suture and the mouth (fig. 46, *c*). To this part one condyle of the mandible articulates.

Although the clypeus almost always appears to be a single sclerite, except when divided transversely as indicated below, it really consists of a transverse row of three sclerites, one on the median line, and one on each side articulating with the mandible. The median sclerite may be designated the *clypeus proper*, and each lateral sclerite, the *antecoxal piece of the mandible*. Usually there are no indications of the sutures separating the clypeus proper from the antecoxal pieces; but in some insects they are distinct. In the larva of *Corydalus*, the antecoxal pieces are not only distinct but are quite large (Fig. 47, *ac*, *ac*).

In some insects the clypeus is completely or partly divided by a transverse suture into two parts (Fig. 45). These may be designated as the *first clypeus* and the *second clypeus*, respectively; the first clypeus being the part next the front (Fig. 45, C_1) and the second clypeus being that next the labrum (Fig. 45, C_2).

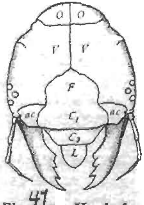

Fig. 47.—Head of a larva of *Corydalus*, dorsal aspect.

The suture between the clypeus and the epicranium is termed the *clypeal suture*.

The labrum.—The *lăbrum* is the movable flap which constitutes the upper lip of the mouth (Fig. 45, *L*). The labrum is the last of the series of unpaired sclerites between the epicranial suture and the mouth. It has the appearance of an appendage but is really a portion of one of the head segments.

The epicranium.—Under the term *epicrānium* are included all of the paired sclerites of the skull, and sometimes also the front. The paired sclerites constitute the sides of

the head and that portion of the dorsal surface that is behind the arms of the epicranial suture. The sclerites constituting this region are so closely united that they were regarded as a single piece by Straus-Durckheim (1828), who also included the front in this region, the epicranial suture being obsolete in the May beetle, which he used as a type.

The vertex.—The dorsal portion of the epicranium; or, more specifically, that portion which is next the front and between the compound eyes is known as the *vertex* (Fig. 45, *V*, *V*). In many insects the vertex bears the paired ocelli. It is not a definite sclerite; but the term vertex is a very useful one and will doubtless be retained.

The occiput.—The hind part of the dorsal surface of the head is the *occiput*. When a distinct sclerite, it is formed from the tergal portion of the united postgenæ described below (Fig. 47, *O*, *O*).

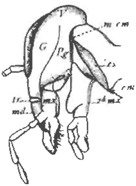

Fig. 48.—Head and neck of a cockroach.

The genæ.—The *genæ* are the lateral portions of the epicranium. Each gena, in the sense in which the word was used by the older writers, includes a portion of several sclerites. Like vertex, however, the term is a useful one.

The postgenæ.—In many insects each gena is divided by a well-marked suture. This led the writer, in an earlier work ('95), to restrict the term *gena* to the part in front of the suture (Fig. 48, *G*), and to propose the term *postgena* for the part behind the suture (Fig. 48, *Pg*).

The gula.—The *gula* is a sclerite forming the ventral wall of the hind part of the head in certain orders of insects, and bearing the labium or second maxillæ (Fig. 49, *Gu*). In the more generalized orders, the sclerite corresponding to the gula does not form a part of the skull. The sutures forming the lateral boundaries of the gula are termed the *gular sutures*.

Fig. 49.—Head of *Corydalus*, adult, ventral aspect.

The ocular sclerites.—In many insects each compound eye is situated in the axis of an annular sclerite; these sclerites bearing the compound eyes are the *ocular sclerites* (Fig. 50, *os*).

The antennal sclerites.—In some insects there is at the base of each antenna an annular sclerite; these are the *antennal sclerites* (Fig. 50, *as*). The antennal sclerites are most distinct in the Plecoptera.

The trochantin of the mandible.—In some insects, as Orthoptera, there is a distinct sclerite between each mandible and the gena; this is the *trochantin of the mandible* (Fig. 45, *tr*).

The maxillary pleurites.—In some of the more generalized insects, as certain cockroaches and crickets, it can be seen that each maxilla is articulated at the ventral end of a pair of sclerites, between which is the invagination that forms the posterior arm of the tentorium; these are the *maxillary pleurites;* the posterior member of this pair of sclerites can be seen in the lateral view of the head of a cockroach (Fig. 48, *m. em*).

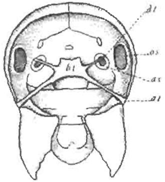

Fig. 50.—Head of a cricket, ental surface of the dorsal wall.

The cervical sclerites.—The *cervical sclerites* are the small sclerites found in the neck of many insects. Of these there are dorsal, lateral, and ventral sclerites. The cervical sclerites were so named by Huxley ('78); recently they have been termed the *intersegmental plates* by Crampton ('17), who considers them to be homologous with sclerites found in the intersegmental regions of the thorax of some generalized insects.

The lateral cervical sclerites have long been known as the *jugular sclerites* (*pièces jugulaires*, Straus Durckheim, 1828).

c. THE APPENDAGES OF THE HEAD

Under this category are classed a pair of jointed appendages termed the *antennæ*, and the organs known collectively as the *mouth-parts*.

The antennæ.—The *antennæ* are a pair of jointed appendages articulated with the head in front of the eyes or between them. The antennæ vary greatly in form; in some insects they are thread-like consisting of a series of similar segments; in others certain segments are greatly modified. The thread-like form is the more generalized

In descriptive works names have been given to particular parts of the antennæ as follows (Fig. 51):

The Scape.—The first or proximal segment of an antenna is called the scape (a The proximal end of this segment is often subglobose, appearing like a distinct segment; in such cases it is called the bulb (a[1]).

The Pĕdicel.—The pedicel is the second segment of an antenna (*b*). In some insects it differs greatly in form from the other segments.

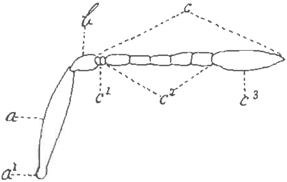

Fig. 51.—Antenna of a chalcis-fly.

The Clăvola.—The term clavola is applied to that part of the antenna distad of the pedicel (*c*); in other words, to all of the antenna except the first and second segments. In some insects certain parts of the clavola are specialized and have received particular names. These are the ring-joints, the funicle, and the club.

The Ring-joints.—In certain insects (*e.g.*, Chalcididæ) the proximal segment or segments of the clavola are much shorter than the succeeding segments; in such cases they have received the name of ring-joints (c^1).

The Club.—In many insects the distal segments of the antennæ are more or less enlarged. In such cases they are termed the club (c^3).

The Fūnicle.—The funicle (c^2) is that part of the clavola between the club and the ring-joints; or, when the latter are not specialized, between the club and the pedicel.

The various forms of antennæ are designated by special terms. The more common of these forms are represented in *Fig.* 52. They are as follows:

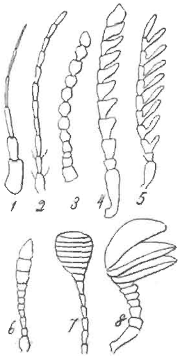

Fig. 52.—Various forms of antennæ.

1. *Setāceous* or bristle-like, in which the segments are successively smaller and smaller, the whole organ tapering to a point.

2. *Fĭliform* or thread-like, in which the segments are of nearly uniform thickness.

3. *Monĭliform* or necklace-form, in which the segments are more or less globose, suggesting a string of beads.

4. *Sĕrrate* or saw-like, in which the segments are triangular and project like the teeth of a saw.

5. *Pĕctinate* or comb-like, in which the segments have long processes on one side, like the teeth of a comb.

6. *Clāvate* or club-shaped, in which the segments become gradually broader, so that the whole organ assumes the form of a club.

7. *Căpitate* or with a head, in which the terminal segment or segments form a large knob.

8. *Lămellate* in which the segments that compose the knob are extended on one side into broad plates.

When an antenna is bent abruptly at an angle like a bent knee (*Fig.* 51) it is said to be *genĭculate*.

The mouth-parts.—The mouth-parts consist typically of an upper lip, *labrum*, an under lip, *labium*, and two pairs of jaws acting horizontally between them. The upper jaws are called the *mandibles;* the lower pair, the *maxillæ*. The maxillæ and labium are each furnished with a pair of feelers, called respectively the *maxillary palpi*, and the *labial palpi*. There may be also within the mouth one or two tongue-like organs, the *epipharynx* and the *hypopharynx*. The mouth-parts of a locust will serve as an example of the typical form of the mouth-parts (Fig. 53).

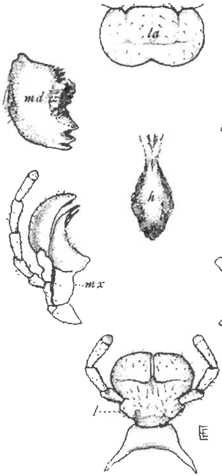

Fig. 53.—Mouth-parts of a locust: *la*, labrum; *md*, mandible; *mx*, maxilla; *h*, hypopharynx; *l*, labium.

The mouth-parts enumerated in the preceding paragraph are those commonly recognized in insects; but in certain insects there exist vestiges of a pair of jaws between the mandibles and the maxillæ, these are the *maxillulæ*.

No set of organs in the body of an insect vary in form to a greater degree than do the mouth-parts. Thus with some the mouth is formed for biting, while with others it is formed for sucking. Among the biting insects some are predaceous, and have jaws fitted for seizing and tearing their prey; others feed upon vegetable matter, and have jaws for chewing this kind of food. Among the sucking insects the butterfly merely sips the nectar from flowers, while the mosquito needs a powerful instrument for piercing its victim. In this chapter the typical form of the mouth-parts as illustrated by the biting insects is described. The various modifications of it presented by the sucking insects are described later, in the discussions of the characters of those insects.

The labrum.—The *lābrum* or upper lip (Fig. 53), is a more or less flap-like organ above the opening of the mouth. As it is often freely movable, it has the appearance of an appendage of the body; but it is not a true appendage, being a part of one of the body segments that enter into the composition of the head.

The mandibles.—The *măndibles* are the upper pair of jaws (Fig. 53). They represent the appendages of one of the segments of the head. In most cases they are reduced to a single segment; but in some insects, as in certain beetles of the family Scarabæidæ, each mandible consists of several more or less distinct sclerites.

The maxillulæ.—The *maxĭllulæ* are a pair of appendages, which when present are situated between the mandibles and the maxillæ. With most insects they are either absent or are so slightly developed that they do not have the appearance of appendages, and have been considered as merely lateral lobes of the hypopharnyx. Borner ('04) finds that the hypopharynx of nearly all insects having an incomplete metamorphosis bears a pair of vestigial maxillulæ; maxillulæ have been found in the Thysanura, Dermaptera, Orthoptera, Corrodentia, the naiads of Ephemerida, and the larvæ of Coleoptera.

In certain Thysanura the maxillulæ are well-preserved; figure 54 represents a maxillula of *Machilis maritima*. These appendages are the "*paraglossæ*" of writers on the Thysanura and Collembola and the *superlinguæ* of Folsom ('00).

The term maxillulæ, a diminutive of maxillæ, was proposed by Hansen ('93), who regards them as homologous with the first maxillæ of the Crustaceæ. They are the appendages of a segment of the head which is very slightly developed in most insects.

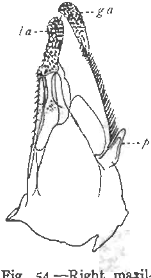

Fig. 54.—Right maxillula of *Machilis maritima*; *la*, lacinia; *ga*, galea; *p*, palpus (After Carpenter).

The maxillæ.—The *maxĭllæ* are the second pair of jaws of most insects, of all insects except those in which the maxillulæ are retained. Like the mandibles they are the appendages of one of the segments of the head.

The maxillæ are much more complicated than the mandibles, each maxilla consisting, when all of the parts are present, of five primary parts and three appendages. The primary parts are the *cardo* or hinge, the *stipes* or foot-stalk, the *palpifer* or palpus-bearer, the *subgalea* or helmet-bearer, and the *lacinia* or blade. The appendages are the *maxillary palpus* or feeler, the *galea*

or superior lobe, and the *digitus* or finger. The maxilla may also bear claw-like or tooth-like projections, spines, bristles, and hairs.

In the following description of the parts of the maxillæ, only very general statements can be made. Not only is there an infinite variation in the form of these parts, but the same part may have a very different outline on the dorsal aspect of the maxilla from what it has on the ventral. Compare Fig. 55 and Fig. 56, which represent the two aspects of the maxilla of *Hydrophilus*. Excepting Fig. 56, the figures of maxillæ represent the ventral aspect of this organ.

The *cardo* or hinge (*a*) is the first or proximal part of the maxilla. It is usually more or less triangular in outline, and is the part upon which nearly all of the motions of this organ depend In many cases, however, it is not the only part directly joined to the body: for frequently muscles extend direct to the subgalea, without passing through the cardo.

The *stipes* or footstalk (*b*) is the part next in order proceeding distad. It is usually triangular, and articulates with the cardo by its base, with the palpifer by its lateral margin, and with the subgalea by its mesal side. In many insects the stipes is united with the subgalea, and the two form the larger portion of the body of the maxilla (Fig. 53). The stipes has no appendages; but the palipfer on the one side, and the subgalea on the other, may become united to the stipes without any trace of suture remaining, and their appendages will then appear to be borne by the stipes. Thus in Fig. 53 it appears to be the stipes that bears the galea, and that receives muscles from the body.

The *pălpifer* or palpus-bearer (*c*) is situated upon the lateral (outer) side of the stipes; it does not, however, extend to the base of this organ, and frequently projects distad beyond it. It is often much more developed on the dorsal side of the maxilla than on the ventral (Figs. 55 and 56). It can be readily distinguished when it is distinct by the insertion upon it of the appendage which gives to it its name.

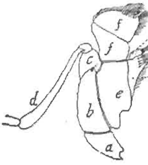

Fig. 55.—Ventral aspect of a maxilla of *Hydrophilus*.

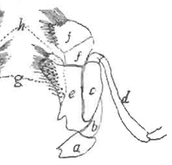

Fig. 56.—Dorsal aspect of a maxilla of *Hydrophilus*.

The *maxillary palpus* or feeler (*d*) is the most conspicuous of the appendages of the maxilla. It is an organ composed of from one to six freely movable segments, and is articulated to the palpifer on the latero-distal angle of the body of the maxilla.

The *subgălea* or helmet-bearer (*e*) when developed as a distinct sclerite is most easily distinguished as the one that bears the galea. It bounds the stipes more or less completely on its mesal (inner) side, and is often directly connected with the body by muscles. In many Coleoptera it is closely united to the lacinia; this gives the lacinia the appearance of bearing the galea, and of being connected with the body (Fig. 56). In several orders the subgalea is united to the stipes; consequently in these orders the stipes appears to bear the galea, and to be joined directly to the body if any part besides the cardo is so connected.

The *gālea* or helmet (*f*) is the second in prominence of the appendages of the maxilla. It consists of one or two segments, and is joined to the maxilla mesad of the palpus. The galea varies greatly in form: it is often more or less flattened, with the distal segment concave, and overlapping the lacinia like a hood. It was this form that suggested the name galea or helmet. In other cases the galea resembles a palpus in form (Fig. 57). The galea is also known as the *outer lobe*, the *upper lobe*, or the *superior lobe*.

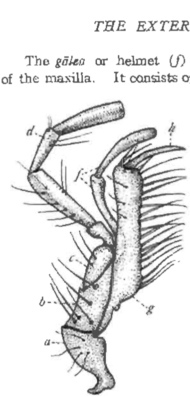

Fig. 57.—Maxilla of *Cicindela*.

The *lacinia* or blade (*g*) is borne on the mesal (inner) margin of the subgalea. It is the cutting or chewing part of the maxilla, and is often furnished with teeth and spines. The lacinia is also known as the *inner lobe*, or the *inferior lobe*.

The *digitus* or finger (*h*) is a small appendage sometimes borne by the lacinia at its distal end. In the Cicindelidæ it is in the form of an articulated claw (Fig. 57); but in certain other beetles it is more obviously one of the segments of the maxilla (Figs. 55 and 56).

The labium or second maxillæ.—The *lābium* or under lip (Fig. 53), is attached to the cephalic border of the gula, and is the most ventral of the mouth-parts. It appears to be a single organ, although sometimes cleft at its distal extremity; it is, however, composed of a pair of appendages grown together on the middle line of the body. In the Crustacea the parts corresponding to the labium of insects consists of two distinct organs, resembling the maxillæ; and in the embryos of insects the labium arises as a pair of appendages.

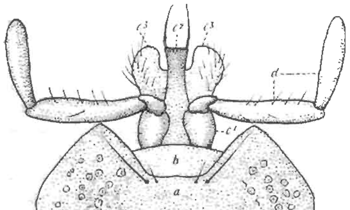

Fig. 58.—Labium of *Harpalus*.

In naming the parts of the labium, entomologists have usually taken some form of it in which the two parts are completely grown together, that is, one which is not cleft on the middle line (Fig. 58). I will first describe such a labium, and later one in which the division into two parts is carried as far as we find it in insects.

The labium is usually described as consisting of three principal parts and a pair of appendages. The principal parts are the *submentum*, the *mentum*, and the *ligula;* the appendages are the *labial palpi.*

The *submentum.* The basal part of the labium consists of two transverse sclerites; the proximal one, which is attached to the cephalic border of the gula, is the *submentum* (*a*). This is often the most prominent part of the body of the labium.

The *mentum* is the more distal of the two primary parts of the labium (*b*). It is articulated to the cephalic border of the submentum, and is often so slightly developed that it is concealed by the submentum.

The *ligula* includes the remaining parts of the labium except the labial palpi. It is a compound organ; but in the higher insects the sutures between the different sclerites of which it is composed are usually obsolete. Three parts, however, are commonly distinguished (Fig. 58), a central part, often greatly prolonged, the *glossa* (c^2) and two parts, usually small membranous projections, one on each side of the base of the glossa, the *paraglossæ* (c^3). Sometimes, however, the paraglossæ are large, exceeding the glossa in size.

The *labial palpi.* From the base of the ligula arise a pair of appendages, the *labial palpi.* Each labial palpus consists of from one to four freely movable segments.

In the forms of the labium just described, the correspondence of its parts to the parts of the maxillæ is not easily seen; but this is much more evident in the labium of some of the lower insects, as for example a cockroach (Fig. 59). Here the organ is very deeply cleft; only the submentum and mentum remain united on the median line; while the ligula consists of two distinct maxilla-like parts. It is easy in this case to trace the correspondence referred to above. Each lateral half of the submentum corresponds to the cardo of a maxilla; each half of the mentum, to the stipes; while the remaining parts of a maxilla are represented by each half of the ligula, as follows: near the base of the ligula there is a part (c^1) which bears the labial palpus; this appears in the figure like a basal segment of the palpus; but in many insects it is easily seen that it is undoubtedly one of the primary parts of the organ; it has been named the *palpiger*, and is the homologue of the palpifer of a maxilla. The trunk of each half of the ligula is formed by a large sclerite (c^4); this evidently corresponds to the subgalea. At the distal extremity of this subgalea of the labium there are two appendages. The lateral one of these (c^3) is the *paraglossa*, and obviously corresponds to the galea. The mesal one (c^2) corresponds to the lacinia or inner lobe. This part is probably wanting in those insects in which the glossa consists of an undivided part; and in this case the glossa probably represents the united and more or less elongated subgaleæ.

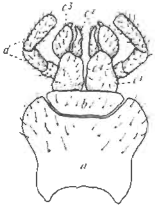

Fig. 59.—Labium of a cockroach.

The epipharnyx.—In some insects there is borne on the ental surface of the labrum, within the cavity of the mouth, an unpaired fold, which is membranous and more or less chitinized: this is the *epiphărynx.*

The hypopharynx.—The *hypophărynx* is usually a tongue-like organ borne on the floor of the mouth cavity. This more simple form of it is well-shown in the Orthoptera (Fig. 53). To the hypopharnyx are articulated the maxillulæ when they are present. The hypopharynx is termed the *lingua* by some writers.

d. THE SEGMENTS OF THE HEAD

The determination of the number of segments in the head of an insect is a problem that has been much discussed since the early days of entomology. The first important step towards its solution was made by Savigny (1816), who suggested that the movable appendages of the head were homodyanmous with legs. This conclusion has been accepted by all; and as each segment in the body of an insect bears only a single pair of appendages, there are at least four segments in the head; *i.e.*, the antennal, the mandibular, the maxillary, and the second maxillary or labial.

In more recent times workers on the embryology of insects have demonstrated the presence of three additional segments. First, there has been found in the embryos of many insects a pair of evanescent appendages situated between the antennæ and the mandibles. These evidently correspond to the second antennæ of Crustacea, and indicate the presence of a second antennal segment in the head of an insect. This conclusion is confirmed by a study of the development of the nervous system. And in the Thysanura and Collembola vestiges of the second antennæ persist in the adults of certain members of these orders.

Second, as the compound eyes are borne on movable stalks in certain Crustacea, it was held by Milne-Edwards that they represent another pair of appendages; but this view has not been generally accepted. It is not necessary, however, to discuss whether the eyes represent appendages or not; the existence of an ocular segment has been demonstrated by a study of the development of the nervous system.

It has been shown that the brain of an insect is formed from three pairs of primary ganglia, which correspond to the three principal divisions of the brain, the *protocerebrum*, the *deutocerebrum*, and the *tritocerebrum*. And it has also been shown that the protocerebrum innervates the compound eyes and ocelli; the deutocerebrum, the antennæ; and the tritocerebrum, the labrum. This demonstrates the existence of three premandibular segments: an ocular segment or protocerebral segment, without appendages, unless the compound eyes represent them; an antennal or deutocerebral segment, bearing antennæ; and a second antennal or tritocerebral segment, of which the labrum is a part, and to which the evanescent appendages between the antennæ and the mandibles doubtless belong. As Viallanes has shown that the tritocerebrum of Crustacea innervates the second antennæ, we are warranted in considering the tritocerebral segment of insects to be the second antennal segment.

Third, the presence of a pair of jaws, the maxillulæ, between the mandibles and the maxillæ has been demonstrated in several widely separated insects. These are doubtless the appendages of a segment, which is so reduced in most insects that it has been overlooked until comparatively recently. Folsom ('00) in his work on the development of the mouth-parts of *Anurida* demonstrated the existence of the pair of primary ganglia pertaining to this segment.

In addition to the maxillular ganglia, which have been almost universally overlooked, and the existence of which has been denied by some writers, the sub-œsophageal ganglion is formed by the union of three pairs of primitive ganglia, pertaining respectively to the mandibular, the maxillary, and the labial segments of the embryo.

LIST OF THE SEGMENTS OF THE HEAD

First, ocular, or protocerebral.
Second, antennal, or deutocerebral.
Third, second antennal, or tritocerebral.
Fourth, mandibular.
Fifth, maxillular.
Sixth, maxillary.
Seventh, labial, or second maxillary.

III. THE THORAX

a. THE SEGMENTS OF THE THORAX

The prothorax, the mesothorax, and the metathorax.—The thorax is the second or intermediate region of the body; it is the region that in nymphs, naiads, and adults bears the organs of locomotion, the legs, and the wings when they are present. This region is composed of three of the body-segments more or less firmly joined together; the segments are most readily distinguished by the fact that each bears a pair of legs. In winged insects, the wings are borne by the second and third segments. The first segment of the thorax, the one next the head, is named the *prothorax;* the second thoracic segment is the *mesothorax;* and the third, the *metathorax.*

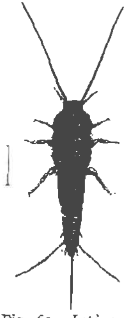

Fig. 60.—*Lepisma saccharina* (After Lubbock).

The simplest form of the thorax in adult insects occurs in the Apterygota (the Thysanura and the Collembola) where although the segments differ in size and proportions, they are distinct and quite similar (Fig. 60).

In the Pterygota, or winged insects, the prothorax is either free or closely united to the mesothorax; in many cases it is greatly reduced in size; it bears the first pair of legs. The mesothorax and the metathorax are more or less closely united, forming a box, which bears the wings and the second and third pairs of legs. This union of these two segments is often so close that it is very difficult to distinguish their limits. Sometimes the matter is farther complicated by a union with the thorax of a part or of the whole of the first

abdominal segment. In the Acridiidæ, for example, the sternum of the first abdominal segment forms a part of the intermediate region of the body, and in the Hymenoptera the entire first abdominal segment pertains to this region.

The alitrunk.—When, as in the Hymenoptera, the intermediate region of the body includes more than the three true thoracic segments it is designated the *ălitrunk*.

The propodeum or the median segment.—When the alitrunk consists of four segments the abdominal segment that forms a part of it is termed the *propōdeum* or the *median segment*. In such cases the true second abdominal segment is termed the first.

b. THE SCLERITES OF A THORACIC SEGMENT

The parts of the thorax most generally recognized by entomologists were described nearly a century ago by Audouin (1824); some additional parts not observed by Audouin have been described in recent times, by the writer ('02), Verhoeff ('03), Crampton ('09), and Snodgrass ('09, '10 *a*, and '10 *b*). The following account is based on all of these works.

In designating the parts of the thorax the prefixes *pro*, *meso*, and *meta* are used for designating the three thoracic segments or corresponding parts of them; and the prefixes *pre* and *post* are used to designate parts of any one of the segments. Thus the scutum of the prothorax is designated the proscutum; while the term prescutum is applied to the sclerite immediately in front of the scutum in each of the thoracic segments. This system leads to the use of a number of hybrid combinations of Latin and Greek terms, but it is so firmly established that it would not be wise to attempt to change it on this account.

Reference has already been made to the division of a body-segment into a tergum, two pleura, and a sternum; each of these divisions will be considered separately; and as the maximum number of parts are found in the wing-bearing segments, one of these will be taken as an illustration.

The sclerites of a tergum.—In this discussion of the external anatomy of the thorax reference is made only to those parts that form the external covering of this region of the body. The infoldings of the body-wall that constitute the internal skeleton are discussed in the next chapter.

The notum.—In nymphs and in the adults of certain generalized insects the tergum of each wing-bearing segment contains a single

chitinized plate; this sclerite is designated the *notum*. The term notum is also applied to the tergal plate of the prothorax and to that of each abdominal segment. The three thoracic nota are designated as the *pronotum*, the *mesonotum*, and the *metanotum* respectively.

The notum of a wing-bearing segment is the part that bears the wings of that segment, even when the tergum contains more than one sclerite. Each wing is attached to two processes of the notum, the *anterior notal process* (Fig. 61, *a n p*) and the *posterior notal process* (Fig. 61, *p n p*); and the posterior angles of the notum are produced into the *axillary cords*, which form the posterior margins of the basal membranes of the wings (Fig. 61, *Ax C*).

The postnotum or postscutellum.—In the wing-bearing segments of most adult insects the tergum consists of two principal sclerites; the notum already described, and behind this a narrower, transverse sclerite which is commonly known as the *postscutĕllum*, and to which Snodgrass has applied the term *postnotum* (Fig. 61, *P N*).

The divisions of the notum.—In most specialized insects the notum of each wing-bearing segment is more or less distinctly divided by transverse lines or sutures into three parts; these are known as the *prescūtum* (Fig. 61, *Psc*), the *scutum* (Fig. 61, *Sct*), and the scutĕllum (Fig. 61, *Scl*).

It has been commonly held, since the days of Audouin, that the tergum of each thoracic segment is composed typically of four sclerites, the prescutum, scutum, scutellum, and postscutellum. But the investigations of Snodgrass indicate that in its more generalized form the tergum contains a single sclerite, the notum; that the postscutellum or postnotum is a secondary tergal chitinization in the dorsal membrane behind the notum, in more specialized insects; and that the separation of the notum into three parts, the prescutum, scutum, and scutellum, is a still later specialization that has arisen independently in different orders, and does not indicate a division into homologous parts in all orders where it exists.

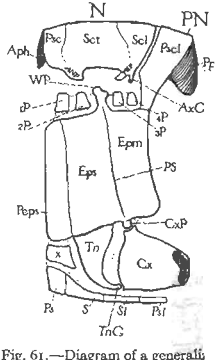

Fig. 61.—Diagram of a generali[zed] thoracic segment (From Sn[od]grass).

The patagia.—In many of the more specialized Lepidoptera the pronotum is produced on each side into a flat lobe, which in some cases is even constricted at the base so as to become a stalked plate, these lobes a[re] the *patāgia*.

The parapsides.—In some Hymenoptera the scutum of the mesothorax is divided into three parts by two longitudinal sutures. The lateral portions of the scutum thus separated from the mesal part are termed the *parăpsides*.

The sclerites of the pleura.—In the accompanying figure (Fig. 61) the sclerites of the left pleurum of a wing-bearing segment are represented diagrammatically; these sclerites are the following:

The episternum.—Each pleurum is composed chiefly of two sclerites, which typically occupy a nearly vertical position, but usually are more or less oblique. In most insects the dorsal end of these sclerites extends farther forward than the ventral end, but in the Odonata the reverse may be true. The more anterior in position of these two sclerites is the *epistĕrnum* (Fig. 61, *Eps*).

In several of the orders of insects one or more of the episterna are divided by a distinct suture into an upper and a lower part. These two parts have been designated by Crampton ('09) as the *anĕpistĕrnum* and the *katĕpistĕrnum* respectively (Fig. 62).

The epimerum.—The *epimērum* is the more posterior of the two principal sclerites of a pleurum (Fig. 61). It is separated from the episternum by the *pleural suture* (Fig. 61, *PS*) which extends from the *pleural wing process* above (Fig. 61, *Wp*) to the *pleural coxal process* below (Fig. 61, *CxP*).

In some of the orders of insects one or more of the epimera are divided by a distinct suture into an upper and a lower part. These two parts have been designated by Crampton ('09) as the *anĕpimērum* and the *katĕpimērum* respectively (Fig. 62).

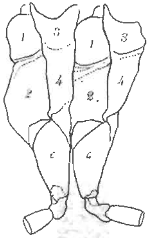

Fig. 62.—Lateral aspect of the meso- and metathorax of *Mantispa rugicollis*; 1, 1, anepisternum; 2, 2, katepisternum; 3, 3, anepimerum; 4, 4, katepimerum; c, c, coxa.

The preepisternum.—In some of the more generalized insects there is a sclerite situated in front of the episternum; this is the *preepistĕrnum* (Fig. 61, *Peps*).

The paraptera.—In many insects there is on each side a small sclerite between the upper end of the episternum and the base of the wing; these have long been known as the *parăptera*. Snodgrass (10 *a*) has shown that there are in some insects two sclerites in this region, which, he designates the *episternal paraptera* or *preparaptera* (Fig. 61, 1*P* and 2*P*); and that one or occasionally two are similarly situated between the epimerun and the base of the wing, the *epimeral paraptera* or *postparaptera* (Fig. 61, 3*P* and 4*P*).

The spiracles.—The external openings of the respiratory system are termed *spiracles*. Of these there are two pairs in the thorax. The first pair of thoracic spiracles open, typically, one on each side in the transverse conjunctiva between the prothorax and the mesothorax; the second pair open in similar positions between the mesothorax and the metathorax. In some cases the spiracles have migrated either forward or backward upon the adjacent segment. For a discussion of the number and distribution of the spiracles, see the next chapter.

The peritremes.—In many cases a spiracle is surrounded by a circular sclerite; such a sclerite is termed a *pĕritreme*.

The acetabula or coxal cavities.—In some of the more specialized insects, as many beetles for example, the basal segment of the legs is inserted in a distinct cavity; such a cavity is termed an *acetăbulum* or *coxal cavity*. When the epimera of the prothorax extend behind the coxæ and reach the prosternum, the coxal cavities are said to be *closed* (Fig. 63); when the epimera do not extend behind the coxa to the prosterum, the coxal cavities are described as *open* (Fig. 64).

The sclerites of a sternum.—In the more generalized insects the sternum of a wing-bearing segment may consist of three or fou sclerites. These have been designated, beginning with the anterio one, the *presternum* (Fig. 61, *Ps*), the *sternum or eusternum* (Fig. 61, *S*), the *sternellum* (Fig. 61, *Sl*), and the *poststernellum* (Fig. 61, *Psl*).

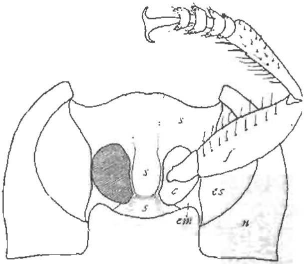

Fig. 63.—Prothorax of *Harpalus*, ventral aspe *c*, coxa; *em*, epimerum; *es*, episternum; femur; *n*, pronotum; *s, s, s*, prosternum.

In the more specialized insects only one of these, the sternum, remains distinctly visible. It is an interesting fact that while in the specialization of the tergum there is an increase in the number of the sclerites in this division of a segment, in the specialization of the sternum there is a reduction.

It is a somewhat unfortunate fact that the term sternum has be used in two senses: first, it is applied to the entire ventral division a segment; and second, it is applied to one of the sclerites enteri

into the composition of this division when it consists of more than a single sclerite. To meet this difficulty Snodgrass has proposed that the term *eusternum* be applied to the sclerite that has been known as the sternum; and that the word sternum be used only to designate the entire ventral division of a segment.

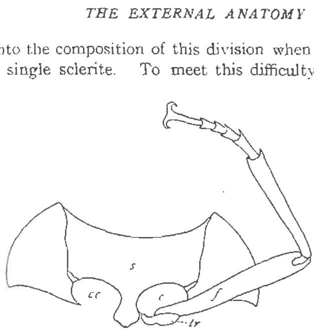

Fig. 64.—Prothorax of *Penthe*; *c*, coxa; *cc*, coxal cavity; *f*, femur; *s*, prosternum; *tr*, trochanter.

C. THE ARTICULAR SCLERITES OF THE APPENDAGES

At the base of each leg and of each wing there are typically several sclerites between the appendage proper and the sclerites of the trunk of the segment; these sclerites, which occupy an intermediate position between the body and its appendage, are termed the *articular sclerites*.

Frequently one or more of the articular sclerites become consolidated with sclerites of the trunk so as to appear to form a part of its wall; this is especially true of those at the base of the legs.

The articular sclerites of the legs.—The proximal segment of the leg, the coxa, articulates with the body by means of two distinct articulations, which may be termed the *pleural articulation of the coxa* and the *ventral articulation of the coxa* respectively. The pleural articulation is with the ventral end of the foot of the lateral apodeme of the segment, *i. e.* with the *pleural coxal process*, which is at the ventral end of the suture between the episternum and the epimerun (Fig. 61, *CxP*). The ventral articulation is with a sclerite situated between the coxa and the episternum; this sclerite and others associated with it may be termed the *articular sclerites of the legs*. The articular sclerites of the legs to which distinctive names have been applied are the following:

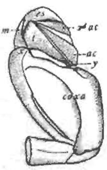

Fig. 65.—The base of a leg of a cockroach.

The trochantin.—The maximum number of articular sclerites of the legs are found in the more generalized insects; in the more specialized insects the number is reduced by a consolidation of some of them with

adjacent parts. The condition found in a cockroach may be taken as typical. In this insect the *trochăntin* (Fig. 65, *t*) is a triangular sclerite, the apex of which points towards the middle line of the body, and is near the ventral articulation of the coxa (Fig. 65, *y*). In most specialized insects the trochantin is consolidated with the antecoxal piece, and the combined sclerites, which appear as one, are termed the trochantin.

The antecoxal piece.—Between the trochantin and the episternum there are, in the cockroach studied, two sclerites; the one next the trochantin is the *antecoxal piece*. This is the articular sclerite that articulates directly with the coxa (Fig. 65, *ac*). As stated above, the antecoxal piece is usually consolidated with the trochantin, and the term trochantin is applied to the combined sclerites. Using the term trochantin in this sense, the statement commonly made that the ventral articulation of the coxa is with the trochantin is true.

The second antecoxal piece.—The sclerite situated between the antecoxal piece and the episternum is the *second antecoxal piece* (Fig. 65, $2^d ac$). This is quite distinct in certain generalized insects; but it is usually lacking as a distinct sclerite.

The articular sclerites of the wings.—In the Ephemerida and Odonata the chitinous wing-base is directly continuous with the walls of the thorax. In all other orders there are at the base of each wing several sclerites which enter into the composition of the joint by which the wing is articulated to the thorax; these may be termed collectively the *articular sclerites of the wings*. Beginning with the front edge of this joint and passing backward these sclerites are as follows:

The tegula.—In several orders of insects there is at the base of the costal vein a small, hairy, slightly chitinized pad; this is the *tegula* (Fig. 66, *Tg*). In the more highly specialized orders, the Lepidoptera, the Hymenoptera, and the Diptera, the tegula is largely developed so as to form a scale-like plate overlapping the base of the wing.

The tegulæ of the front wings of Lepidoptera are specially large and are carried by special *tegular plates* of the notum. These, in turn, are supported by special internal *tegular arms* from the bases of the pleural wing-processes (Snodgrass, '09)

The axillaries.—Excepting the tegula, which is at the front edge of the wing-joint, the articular sclerites of the wings have been termed collectively the *axillaries*. Much has been written about these sclerites, and many names have been applied to them. The simplest terminology is that of Snodgrass ('09 and '10 *a*) which I here adopt.

The first axillary.—This sclerite (Fig. 66, 1 *Ax*) articulates with the anterior notal wing-process and is specially connected with the base of the subcostal vein of the wing. In rare cases it is divided into two.

The second axillary.—The second axillary (Fig. 66, 2 *Ax*) articulates with the first axillary proximally and usually with the base of the radius distally; it also articulates below with the wing-process of the pleurum, constituting thus a sort of pivotal element.

The third axillary.—The third axillary (Fig. 66, 3 *Ax*) is interposed between the bases of the anal veins and the fourth axillary when this sclerite is present. When the fourth axillary is absent, as it is in

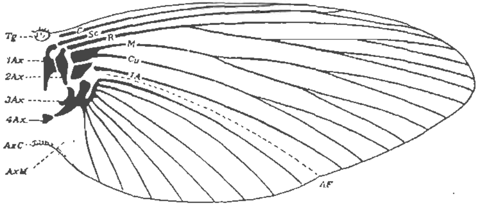

Fig. 66.—Diagram of a generalized wing and its articular sclerites (From Snodgrass).

nearly all insects except Orthoptera and Hymenoptera, the third axillary articulates directly with the posterior notal wing-process.

The fourth axillary.—When this sclerite is present it articulates with the posterior notal wing-process proximally and with the third axillary distally (Fig. 66, 4 *Ax*). Usually this sclerite is absent; it occurs principally in Orthoptera and Hymenoptera.

The median plates.—The median plates of the wing-joint are not of constant shape and occurrence; when present, these plates are associated with the bases of the media, the cubitus, and the first anal vein when the latter is separated from the other anals. Often one of them is fused with the third axillary and sometimes none of them are present.

d. THE APPENDAGES OF THE THORAX

The appendages of the thorax are the organs of locomotion. They consist of the *legs* and the *wings*. Of the former there are three

pairs, a pair borne by each of the three thoracic segments; of the latter there are never more than two pairs, a pair borne by the mesothorax and a pair borne by the metathorax. One or both pairs of wings may be wanting.

The legs.—Each leg consists of the following named parts and their appendages: *coxa*, *trochanter*, *femur*, *tibia*, and *tarsus*.

The coxa.—The coxa is the proximal segment of the leg; it is the one by which the leg is articulated to the body (Fig. 67). The coxa varies much in form, but it is usually a truncated cone or nearly globular. In some insects the coxæ of the third pair of legs are more or less flattened and immovably attached to the metasternum; this is the case in beetles of the family Carabidæ for example. In such cases the coxæ really form a part of the body-wall, and are liable to be mistaken for primary parts of the metathorax instead of the proximal segments of appendages.

In several of the orders of insects the coxa is apparently composed of two, more or less distinct, parallel parts; this is the case, for example, in insects of the trichopterous genus *Neuronia* (Fig. 68, *Cx* and *epm*) But it has been shown by Snodgrass ('09) that the posterior part of the supposed double coxa (Fig. 68 *epm*) is a detached portion of the epimerum, the katepimerum

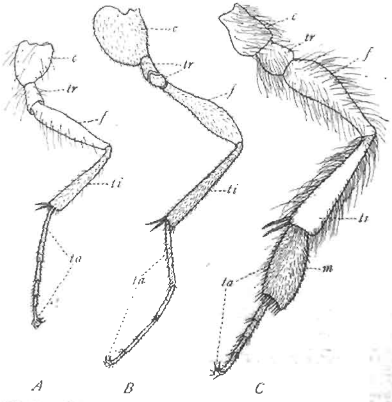

Fig. 67.—*Legs of insects*: A, *wasp*; B, *ichneumon-fly*; C, *bee*; *c*, coxa; *tr*, trochanter; *f*, femur; *ti*, tibia; *ta*, tarsus; *m*, metatarsus.

The styli—In certain generalized insects, as *Machilis* of the orde

Thysanura, the coxa of each middle and hind leg bears a small appendage, the *stylus* (Fig. 69). The styli are of great interest as they are believed to correspond to one of the two branches of the legs of Crustacea; thus indicating that insects have descended from forms in which the legs were biramous.

In several genera of the Thysanura one or more of the abdominal segments bear each a pair of styli; in *Machilis* they are found on the second to the ninth abdominal segments. These styli are regarded as vestiges of abdominal legs.

The trochanter.—The trochănter is the second part of the leg. It consists usually of a very short, triangular or quadrangular segment, between the coxa and the femur. Sometimes the femur appears to articulate directly with the coxa; and the trochanter to be merely an appendage of the proximal end of the femur (*e. g.* Carabidæ). But the fact is that in these insects, although the femur may touch the coxa, it does not articulate with it; and the organs that pass from the cavity of the coxa to that of the femur must pass through the trochanter. In some Hymenoptera the trochanter consists of two segments (67, *B*).

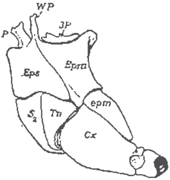

Fig. 68.—Lateral aspect of the mesothorax of *Neuronia* (From Snodgrass).

The femur.—The femur is the third part of the leg; and is usually the largest part. It consists of a single segment.

The tibia.—The tibia is the fourth part of the leg. It consists of a single segment; and is usually a little more slender than the femur, although it often equals or exceeds it in length. In such species as burrow in the ground, the distal extremity is greatly broadened and shaped more or less like a hand. Near the distal end of the tibia there are in most insects one or more spurs, which are much larger than the hairs and spines which arm the leg; these are called the *tibial spurs*, and are much used in classification.

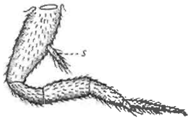

Fig. 69.—A leg of *Machilis*; *s*, stylus.

The tarsus.—The tarsus is the fifth and most distal part of the leg, that which is popularly called the foot. It consists of a series of segments, varying in number from one to six. The most common number of segments in the tarsus is five.

In many insects, the first segment of the tarsus is much longer,

and sometimes much broader, than the other segments. In such cases this segment is frequently designated as the *metatarsus* (Fig. 67, *C*, *m*).

In some insects the claws borne by the distal end of the tarsus are outgrowths of a small terminal portion of the leg, the sixth segment of the tarsus of some authors. This terminal part with its appendages has received the name *prætarsus* (De Meijere '01). As a rule the prætarsus is withdrawn into the fifth segment of the tarsus or is not present as a distinct segment.

On the ventral surface of the segments of the tarsus in many insects are cushion-like structures; these are called *pulvilli*. The cuticula of the pulvilli is traversed by numerous pores which open either at the surface of the cuticula or through hollow hairs, the *tenent-hairs*, and from which exudes an adhesive fluid that enables the insect to walk on the lower surface of objects.

With many insects (*e. g.* most Diptera) the distal segment of the tarsus bears a pair of pulvilli, one beneath each claw. In such cases there is frequently between these pulvilli a third single appendage of similar structure; this is called the *empōdium;* writers on the Orthoptera commonly called the appendage between the claws the *arolium*. In other insects the empodium is bristle-like or altogether wanting.

In many insects the pulvillus of the distal segment of the tarsus is a circular pad projecting between the tarsal claws. In many descriptive works this is referred to as *the* pulvillus, even though the other pulvilli are well-developed. The pulvilli are called the *onȳchii* by some writers.

The claws borne at the tip of the tarsus are termed the *tarsal claws* or *ungues;* they vary much in form; they are usually two in number, but sometimes there is only one on each tarsus.

The wings.—The wings of insects are typically two pairs of membranous appendages, one pair borne by the mesothorax and one pair by the metathorax; prothoracic wings are unknown in living insects but they existed in certain paleozoic forms.

Excepting in the subclass Apterygota, which includes the orders Thysanura and Collembola, wings are usually present in adult insects. Their absence in the Apterygota is due to the fact that they have not been evolved in this division of the class Hexapoda; but when they are absent in adult members of the subclass Pterygota, which includes the other orders of insects, their absence is due to a degradation, which has resulted in their loss.

The loss of wings is often confined to one sex of a species; thus with the canker-worm moths, for example, the females are wingless, while the males have well-developed wings; on the other hand, with the fig-insects, *Blastŏphaga,* the female is winged and the male wingless.

Studies of the development of wings have shown that each wing is a saclike fold of the body-wall; but in the fully developed wing, its saclike nature is not obvious; the upper and lower walls become closely applied throughout the greater part of their extent; and since they become very thin, they present the appearance of a single delicate membrane. Along certain lines, however, the walls remain separate, and are thickened, *forming the firmer framework of the wing.* These thickened and hollow lines are termed the *veins* of the wing; and their arrangement is described as the *venation* of the wing.

The thin spaces of the wings which are bounded by veins are called *cells.* When a cell is completely surrounded by veins it is said to be *closed;* and when it extends to the margin of the wing it is said to be *open.*

The different types of insect wings.—What may be regarded as the typical form of insect wing is a nearly flat, delicate, membranous appendage of the body, which is stiffened by the so-called wing-veins; but striking modifications of this form exist; and to certain of them distinctive names have been applied, as follows:

In the Coleoptera and in the Dermaptera, the front wings are thickened and serve chiefly to protect the dorsal wall of the body and the membranous hind wings, which are folded beneath them when not in use. Front wings of this type are termed wing-covers or *ĕlytra.*

The front wings of the Heteroptera, which are thickened at the base like elytra, are often designated the *hemĕlytra.*

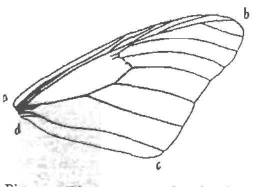

Fig. 70.—Diagram of a wing showing margins and angles.

The thickened fore wings of Orthoptera are termed *tĕgmina* by many writers.

The hind wings of Diptera, which are knobbed, thread-like organs, are termed *haltēres.* The hind wings of the males of the family Coccidæ are also thread-like.

The reduced front wings of the Strepsiptera are known as the *pseudo-haltēres.*

The margins of wings.—Most insect wings are more or less triangular in outline; they, therefore, present three margins: the *costal margin* or *costa* (Fig. 70, *a-b*); the *outer margin* (Fig. 70, *b-c*); and the *inner margin* (Fig. 70, *c-d*).

The angles of wings.—The angle at the base of the costal margin of a wing is the *humeral angle* (Fig. 70, *a*); that between the costal margin and the outer margin is the *apex* of the wing (Fig. 70, *b*);

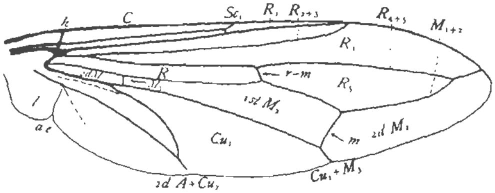

Fig. 71.—Wing of *Conops*; *ae*, axillary excision; *l*, posterior lobe.

and that between the outer margin and the inner margin is the *anal angle* (Fig. 70, *c*).

The axillary cord.—The posterior margin of the membrane at the base of the wing is usually thickened and corrugated; this cord-like structure is termed the *axillary cord*. The axillary cord normally arises, on each side, from the posterior lateral angle of the notum, and thus serves as a mark for determining the posterior limits of the notum.

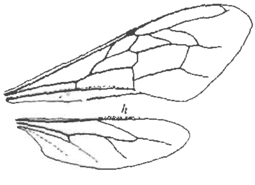

Fig. 72.—Wings of the honeybee; *h*, hamuli.

The axillary membrane.—The membrane of the wing base is termed the axillary membrane; it extends from the tegula at the base of the costal margin to the axillary cord; in it are found the axillary sclerites.

The alula.—In certain familie[s] of the Diptera and of the Coleop[-] tera the axillary membrane i[s] expanded so as to form a lobe o[r] lobes which fold beneath the base of the wing when the wings ar[e] closed; this part of the wing is the *alula* or *alulet*. The alulæ ar[e] termed the *squamæ* by some writers, and the *calypteres* by others.

The axillary excision.—In the wings of most Diptera and in the wings of many other insects there is a notch in the inner margin of the wing near its base (Fig. 71, *ae*), this is the *axillary excision.*

The posterior lobe of the wing.—That part of the wing lying between the axillary excision when it exists, and the axillary membrane is the *posterior lobe* of the wing. The posterior lobe of the wing and an alula are easily differentiated as the alula is margined by the axillary cord.

The methods of uniting the two wings of each side.—It is obvious that a provision for ensuring the synchronous action of the fore and hind wings adds to their efficiency; it is as important that the two pairs of wings should act as a unit as it is that the members of a boat's crew should pull together. In many insects the synchronous action of the wings is ensured by the fore wing overlapping the hind wing. But in other insects special structures have been developed which fasten together the two wings of each side. The different types of these structures have received special names as follows:

The hamuli.—With certain insects the costal margin of the hind wings bears a row of hooks, which fasten into a fold on the inner margin of the fore wings (Fig. 72); these hooks are named the *hămuli.*

The frenulum and the frenulum hook.—In most moths there is a strong spine-like organ or a bunch of bristles borne by the hind wing at the humeral angle (Fig. 73, *f*); this is the *frenulum* or little bridle. As a rule the frenulum of the female consists of several bristles; that of the male, of a single, strong, spine-like organ. In the males of certain moths, where the frenulum is highly developed, there is a membranous fold on the fore wing for receiving the end of the frenulum, this is the *frenulum hook* (Fig. 73, *fh*).

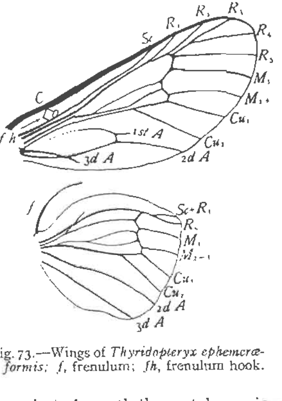

Fig. 73.—Wings of *Thyridopteryx ephemeræformis*; *f*, frenulum; *fh*, frenulum hook.

The jugum.—In one family of moths, the Hepialidæ, the posterior lobe of the fore wing is a slender, finger-like organ which is stiffened by a branch of the third anal vein, and which projects beneath the costal margin of the hind wing. As the greater part of the inner margin of the fore

wing overlaps the hind wing, the hind wing is held between the two (Fig. 74). This type of the posterior lobe of the fore wing is termed the *jugum* or yoke. The structure of the jugum is shown in Figure 75.

The fibula.—In several groups of insects an organ has been developed that serves to unite the fore and hind wings, but which functions in a way quite different from that of the jugum. Like the jugum it is found at the base of the fore wing; but unlike the jugum it extends back above the base of the hind wing and is clasped over an elevated part of the hind wing; this organ is the *fibula* or clasp.

In some insects, as in the Trichoptera, the fibula consists only of a specialized posterior lobe of the fore wing; in others, as in the genus *Corydalus* of the order Neuroptera, the proximal part of the fibula is margined by the axillary cord, showing that the axillary membrane enters into the composition of this organ (Fig. 76).

The hypothetical type of the primitive wing-venation.—A careful study of the wings of many insects has shown that the fundamental type of venation is the same in all of the orders of winged insects. But this fact is evident only when the more primitive or generalized members of different orders are compared with each other. In most of the orders of insects the greater number of species have become so modified or specialized as regards the structure of their wings that it is difficult at first to trace out the primitive type.

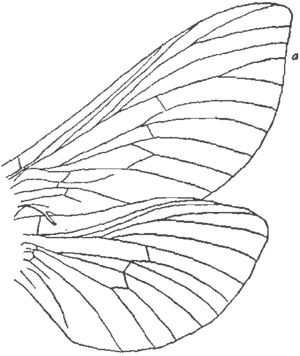

Fig. 74.—Wings of a hepialid, seen from below: *a*, accessory vein.

This agreement in the important features of the venation of the wings of the generalized members of the different orders of insects is still more evident when the wings of nymphs, naiads and pupæ are studied. It has been demonstrated that in the development of wings of generalized insects the longitudinal wing-veins are formed about preexisting tracheæ. In the development of the wing, the tracheæ grow out into the wing-bud, and later the wing-veins are formed about them.

The wings of nymphs, naiads, and pupæ are broad at the base, and consequently the tracheæ that precede the wing-veins are not crowded together as are the wing-veins at the base of the wings of

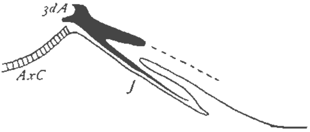

Fig. 75.—Jugum of a hepialid.

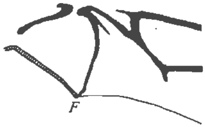

Fig. 76.—Fibula of *Corydalus*.

adults. For this reason the identity of the wing-veins can be determined more surely in the wings of immature insects than they can be in the wings of adults. This is especially true where two or more veins coalesce in the adult wing while the tracheæ that precede these veins are distinctly separate in the immature wing.

A study was made of the tracheation of the wings of immature insects of representatives of most of the orders of insects, and, assuming that those features that are possessed by all of them must have been inherited from a common ancestor, a diagram was made representing the hypothetical tracheation of a nymph of the primitive winged insect (Fig. 77). In this diagram the tracheæ are lettered

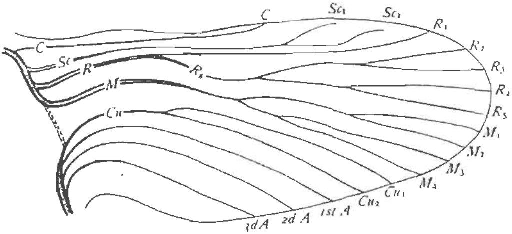

Fig. 77.—Hypothetical tracheation of a wing of the primitive nymph.

with the abbreviations used in designating the veins that are formed about them in the course of the development of the wing. The diagram will serve, therefore, to indicate the typical venation of an insect

wing, except that the tracheæ are not crowded together at the base of the wing as are the veins in the wings of adults.*

Longitudinal veins and cross-veins.—The veins of the wing can be grouped under two heads: first, *longitudinal veins,* those that normally extend lengthwise the wing; and second, *cross-veins,* those that normally extend in a transverse direction.

The insertion of the word *normally* in the above definitions is important; for it is only in comparatively generalized wings that the direction of a vein can be depended upon for determining to which of these two classes it belongs.

The principal wing-veins.—The longitudinal wing-veins constitute the principal framework of the wings. In the diagram representing the typical venation of an insect wing (Fig. 77), only longitudinal veins are indicated; this is due to the fact that the diagram was based on a study of the tracheation of wings, and in the more generalized wings the cross-veins are not preceded by tracheæ; moreover in the wings of more generalized paleozoic insects there were no definite cross-veins, but merely an irregular network of thickened lines between the longitudinal veins.

There are eight principal veins; and of these the second, third, fourth, and fifth are branched. The names of these veins and the abbreviations by which they are known are as follows, beginning with the one nearest the costal margin of the wing:

Names of veins	*Abbreviations*
Costa	C
Subcosta	Sc
Radius	R
Media	M
Cubitus	Cu
First Anal	1st A
Second Anal	2d A
Third Anal	3d A

The chief branches of the wing-veins.—The chief branches of the principal veins are numbered, beginning with the branch nearest the costal margin of the wing. The term used to designate a branch of a vein is formed by compounding the name of the vein with

*For many details regarding the development of the wings of insects, the structure, and the terminology of the wing-veins, that can not be included in this work, see a volume by the writer entitled *The Wings of Insects.* This is published by The Comstock Publishing Company, Ithaca, N. Y.

numeral indicating the number of the branch; thus, for example, the first branch of the radius is radius-one or vein R_1.

In the case of radius and media, each of which has more than two branches, each division of the vein that bears two or more branches has received a special name. Thus after the separation of radius-one from the main stem of radius there remains a division which is typically four-branched; this division is termed the radial sector, or vein R_s; the first division of the radial sector, which later separates into radius-two and radius-three, is designated as radius-two-plus-three or vein R_{2+3}; and the second division is termed radius-four-plus-five or vein R_{4+5}. Media is typically separated into two divisions, each of which is two-branched; the first division is media-one-plus two or vein M_{1+2}, the second is media-three-plus-four or vein M_{3+4}.

The veins of the anal area.—The three anal veins exhibit a wide range of variation both as to their persistence and to their form when

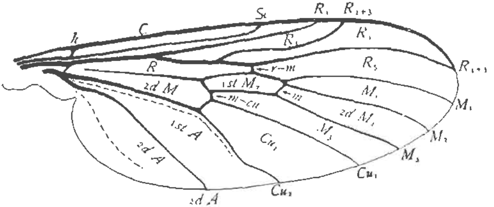

Fig. 78.—A wing of *Rhyphus*.

present. In those cases where the anal veins are branched there is no indication that the branching has been derived from a uniform primitive type of branching. For this reason in describing a branched anal vein merely the number of branches is indicated.

In some cases, as in the Odonata, there is a single anal vein the identity of which can not be determined. In such cases this vein is designated merely as the *anal vein* or *vein A*, and its branches as A_1, A_2, A_3, *etc.*

The reduction of the number of wing-veins.—In many wings the number of the veins is less than it is in the hypothetical type. In some cases this is due to the fact that one or more veins have faded out in the course of the evolution of the insects showing this deficiency; frequently in such wings vestiges of the lacking veins remain, either as faint lines in the positions formerly occupied by the veins or as

short fragments of the veins. A much more common way in which the number of veins has been reduced is by the coalescence of adjacent veins. In many wings the basal parts of two or more principal veins are united so as to appear as a single vein; and the number of the branches of a vein has been reduced in very many cases by two or more branches becoming united throughout their entire length.

When a vein consists of two or more of the primitive veins united, the name applied to the compound vein should indicate this fact. In the wing of *Rhyphus* (Fig. 78), for example, radius is only three-branched; but it would be misleading to designate these branches as R_1, R_2, and R_3, for this would indicate that veins R_4 and R_5 are lacking. The first branch is evidently R_1; the second branch is composed of the

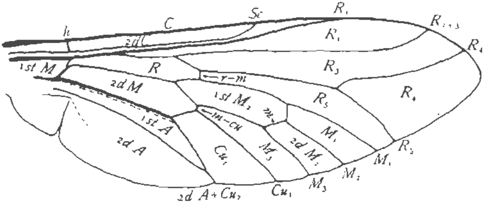

Fig. 79.—A wing of *Tabanus*.

coalesced R_2 and R_3, it is, therefore, designated as R_{2+3}; and the third branch, which consists of the coalesced R_4 and R_5, is designated as R_{4+5}.

A second method of coalescence of veins is illustrated by a wing of *Tabanus* (Fig. 79). In this wing the tips of cubitus-two and the second anal vein are united; here the coalescence began at the margin of the wing and is progressing towards the base. The united portions of the two veins are designated as 2d A_+Cu_2.

When it is desired to indicate the composition of a compound vein it can be readily done by combining the terms indicating its elements. But in descriptions of hymenopterous wings where a compound vein may be formed by the coalescence of several veins the logical carrying out of this plan would result in a very cumbersome terminology, one that it is impracticable to use in ordinary descriptions. In such cases the compound vein is designated by the term indicating its most obvious element. Thus, for example, in the fore

wing of *Pamphilius*, where veins M_4, Cu_1, and Cu_2 coalesce with the first anal vein, the united tips of these veins is designated as vein 1st A, the first anal vein being its most obvious element (Fig. 80), although it is really vein $M_4+Cu_1+Cu_2+$1st A.

Serial veins.—In the wings of some insects, where the wing-venation has been greatly modified, as in certain Hymenoptera, there exist what appears to be simple veins that in reality are compound veins composed of sections of two or more veins joined end to end with no indication of the point of union. Compound veins formed in this

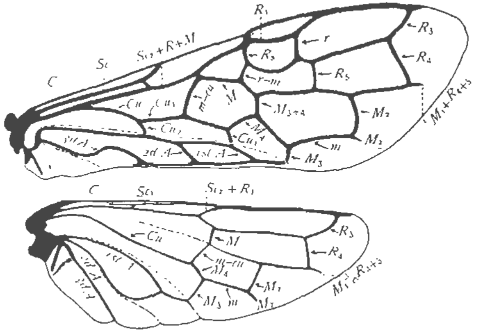

Fig. 80.—Wings of *Pamphilius*.

manner are termed *serial veins*. Examples of wings in which there are serial veins are figured in the chapter treating of the Hymenoptera.

In designating serial veins either the sign & or a dash is used between the terms indicating the elements of the vein, instead of the sign + as the latter is used in designating compound veins formed by the coalescence of veins side by side. If the serial vein consists of only two elements the sign & is used; thus the serial vein in the wings of braconids, which consists of the medial cross-vein and vein M_2, is designated as m & M_2.

In those cases where sections of several veins enter into the composition of a serial vein, the serial vein is designated by the abbreviation of the name of the basal element connected by a dash with the

abbreviation of the name of the terminal element. Thus a serial vein, the basal element of which is the cubitus and the terminal element vein M_1, is designated as vein $Cu—M_1$. A serial vein thus formed exists in the hind wings of certain ichneumon flies.

The increase of the number of wing-veins. In the wings of many insects the number of veins is greater than it is in the hypothetical type. *This multiplication of veins is due either to an increase in the*

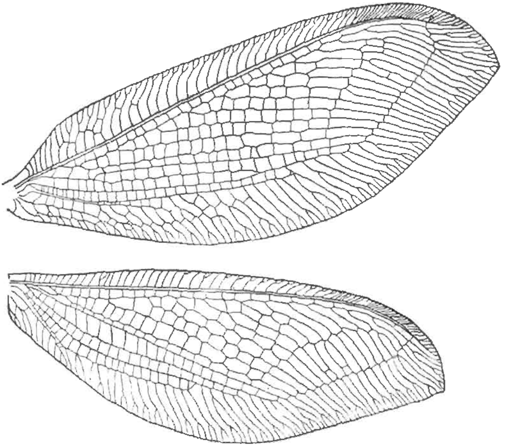

Fig. 81.—Wings of *Osmylus hyalinatus.*

number of the branches of the principal veins by the addition of secondary branches, termed accessory veins, or to the development of secondary longitudinal veins between these branches, termed intercalary veins. In no case is there an increase in the number of principal veins.

The accessory veins.—The wings of *Osmylus* (Fig. 81) are an example of wings in which accessory veins have been developed; here the radial sector bears many more branches than the typical number; those branches that are regarded as the primitive branches are lettered R_1, R_2, R_3, R_4, and R_5 respectively (Fig. 82); the other

branches are the secondarily developed accessory veins. Two types of accessory veins are recognized the *marginal accessory veins* and the *definitive accessory veins*.

The *marginal accessory veins* are twig-like branches that are the result of bifurcations of veins that have not extended far back from the margin of the wing; many such short branches of veins exist in the wings of *Osmylus* (Fig. 81). The number and position of the marginal accessory veins are not constant, differing in the wings of the two sides of the same individual.

The *definitive accessory veins* differ from the marginal accessory

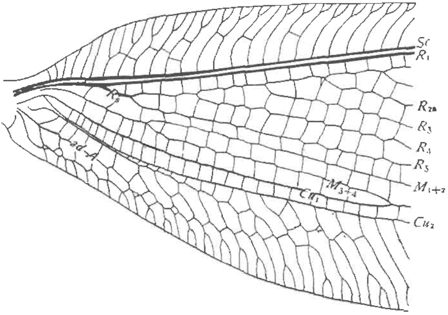

Fig. 82.—Base of fore wing shown in Figure 81

veins in having attained a position that is comparable in stability to that of the primitive branches of the principal veins.

In those cases where the accessory veins are believed to have been developed in regular order they are designated by the addition of a letter to the abbreviation of the name of the vein that bears them; thus if vein R_2 bears three accessory veins they are designated as veins R_{2a}, R_{2b}, and R_{2c}, respectively.

The intercalary veins.—The intercalary veins are secondarily developed longitudinal veins that did not arise as branches of the primitive veins, but were developed in each case as a thickened fold in a corrugated wing, more or less nearly midway between two preexisting veins, with which primarily it was connected only by cross-veins. Excellent examples of unmodified intercalary veins are com-

mon in the Ephemerida, where most of the intercalary veins remain distinct from the veins between which they were developed, being connected with them only by cross-veins, the proximal end of the intercalary vein being free (Fig. 83).

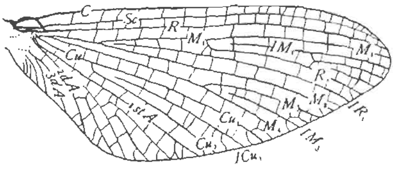

Fig. 83.—Wings of a May-fly (After Morgan).

When it is desirable to refer to a particular intercalary vein it can be done by combining the initial *I*, indicating intercalary, with the designation of the area of the wing in which the intercalary vein occurs. For example, in the wings of most May-flies there is an intercalary vein between veins Cu_1 and Cu_2, *i.e.* in the area Cu_1; this intercalary vein is designated as ICu_1.

The adventitious veins.—In certain insects there are secondary veins that are neither accessory veins nor intercalary veins as defined above; these are termed *adventitious veins*. Examples of these are the *supplements* of the wings of certain Odonata and the *spurious vein* of the Syrphidæ.

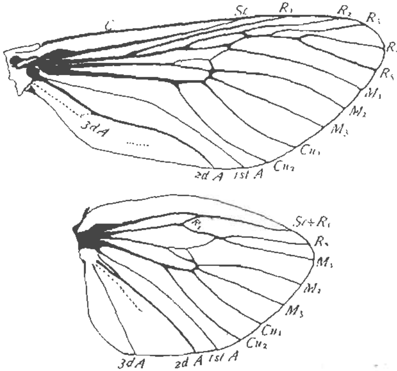

Fig. 84.—Wings of *Prionoxystus*.

The anastomosis of veins.—The typical arrangement of wing-vein is often modified by an anastomosis of adjacent veins; that is, tw

veins will come together at some point more or less remote from their extremities and merge into one for a greater or less distance, while their extremities remain separate. In the fore wing of *Prionoxystus* (Fig. 84), for example, there is an anastomosis of veins R_3 and R_{4+5}.

The named cross-veins.—In the wings of certain insects, as the dragon-flies, May-flies, and others, there are many cross-veins; it is impracticable in cases of this kind to name them. But in several of the orders of insects there are only a few cross-veins, and these have been named. Figure 85 represents the hypothetical primitive type

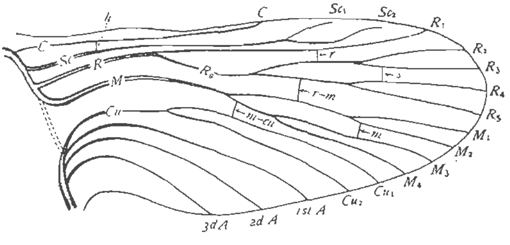

Fig. 85.—The hypothetical primitive type of wing-venation with the named cross-veins added.

of wing-venation with the named cross-veins added in the positions in which they normally occur; these are the following:

The humeral cross-vein (*h*) extends from the subcosta to costa near the humeral angle of the wing.

The *radial cross-vein* (*r*) extends between the two principal divisions of radius, *i. e.* from vein R_1 to vein R_2.

The *sectorial cross-vein* (*s*) extends between the principal divisions of the radial sector— *i. e.*, from vein R_{2+3} to vein R_{4+5} or from vein R_3 to vein R_4.

The *radio-medial cross-vein* (*r—m*) extends from radius to media, usually near the center of the wing. When in its typical position this cross-vein extends from vein R_{4+5} to vein M_{1+2}.

The *medial cross-vein* (*m*) extends from vein M_2 to vein M_3. This cross-vein divides cell M_2 into cells, 1st M_2 and 2d M_2; see Figure 87 where the cells are lettered.

The *medio-cubital cross-vein* (*m—cu*) extends from media to cubitus.

The arculus.—In many insects there is what appears to be a cross-vein extending from the radius to the cubitus near the base of the wing; this is the *arculus*. The arculus is designated in figures of wings by the abbreviation *ar*. Usually when the arculus is present the media appears to arise from it; the fact is, the arculus is compound, being composed of a section of media and a cross-vein.

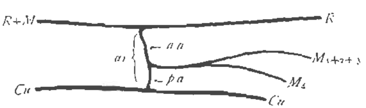

Fig. 86.—Diagram of an arculus of a dragon-fly.

Figure 86 is a diagram representing the typical structure of the arculus. That part of the arculus which is a section of media is designated as the *anterior arculus* (*aa*) and that part formed by a cross-vein, the *posterior arculus* (*pa*).

The terminology of the cells of the wing.—Each cell of the wing is designated by the name of the vein that normally forms its front margin when the wings are spread. See Figure 87 where both the veins and the cells of the wing are lettered.

The cells of the wing fall naturally into two groups: first, those on the basal part of the wing; and second, those nearer the distal end of the wing. The former are bounded by the stems of the principal veins, the latter, by the branches of these veins; a corresponding distinction is made in designating the cells. Thus a cell lying behind the main stem of radius and in the basal part of the wing is designated as cell R; while a cell lying behind radius-one is designated as cell R_1.

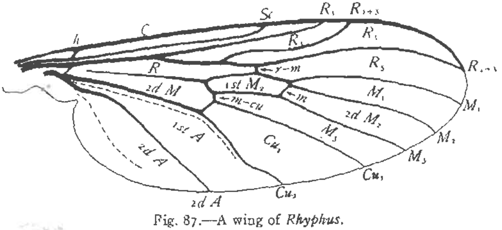

Fig. 87.—A wing of *Rhyphus*.

It should be remembered that the coalescence of two veins result ... of the cell that was between them. Thus whe

veins R_2 and R_3 coalesce, as in the wings of *Rhyphus* (Fig. 87), the cell lying behind vein R_{2+3} is cell R_3, and not cell R_{2+3}, cell R_2 having been obliterated.

When one of the principal cells is divided into two or more parts by one or more cross-veins, the parts may be numbered, beginning with the proximal one. Thus in *Rhyphus* (Fig. 87), cell M_2 is divided by the medial cross-vein into cell *1st*M_2 and cell *2d*M_2.

When two or more cells are united by the atrophy of the vein or veins separating them, the compound cell thus formed is designated by a combination of the terms applied to the elements of the compound cell. When, for example, the stem of media is atrophied, the cell resulting from the combination of cells R and M is designated as cell $R+M$.

The application of this system of naming the cells of the wing is an easy matter in those orders where there are but few cross-veins; but in those orders where there are many cross-veins it is not practicable to apply it. In the latter case we have to do with *areas* of the wing rather than with separate cells. These areas are designated as are the cells of the few-veined wings with which they correspond; thus the area immediately behind vein R_2 is area R_2.

The corrugations of the wings.—The wings of comparatively few insects present a flat surface; in most cases the membrane is thrown into a series of folds or corrugations. This corrugating of the wing in some cases adds greatly to its strength, as in the wings of dragon-flies; in other cases the corrugations are the result of a folding of the wing when not in use, as in the anal area when this part is broadly expanded.

It rarely happens that there is occasion to refer to individual members of either of these classes of folds, except perhaps the one between the costa and the radius, which is the *subcostal fold* and that which is normally between the cubitus and the first anal vein, the *cubito-anal fold*.

Convex and concave veins.—When the wings are corrugated, the wing-veins that follow the crests of ridges are termed *convex veins*; and those that follow the furrows, *concave veins*.

The furrows of the wing.—There are found in the wings of many insects one or more suture-like grooves in the membrane of the wing; these are termed the furrows of the wing. The more important of these furrows are the four following:

The *anal furrow* when present is usually developed in the cubito anal fold; but in the Heteroptera it is found in front of the cubitus.

The *median furrow* is usually between radius and media.

The *nodal furrow* is a transverse suture beginning at a point in the costal margin of the wing corresponding to the nodus of the Odonata and extending towards the inner margin of the wing across a varying number of veins in the different orders of insects.

The *axillary furrow* is a line that serves as a hinge which facilitates the folding of the posterior lobe of the wing of many insects under that part of the wing in front of it.

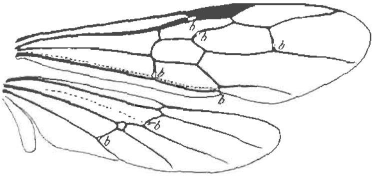

Fig. 88.—Wings of *Myrmecia*: *b*, *b*, *b*, bullæ.

The bullæ.—The *bullæ* are weakened places in veins of the wing where they are crossed by furrows. The bullæ are usually paler in color than the other portions of the wing; they are common in the wings of the Hymenoptera (Fig. 88), and of some other insects.

The ambient vein.—Sometimes the entire margin of the wing is stiffened by a vein-like structure; this is known as the *ambient vein*.

The humeral veins.—In certain Lepidoptera and especially in the Lasiocampidæ, the humeral area of the hind wings is greatly expanded and in many cases is strengthened by the development of secondary veins. These are termed the *humeral veins*.

The pterostigma or stigma.—A thickened, opaque spot which exists near the costal margin of the outer part of the wing in many insects is known as the *pterostigma* or *stigma*.

The epipleuræ.—A part of the outer margin of the elytra of beetles when turned down on the side of the thorax is termed the *epipleura*.

The discal cell and the discal vein.—The term *discal cell* is applied to a large cell which is situated near the center of the wing; and the term *discal vein*, to the vein or series of veins that limits the outer end of the discal cell. These terms are not a part of the uniform terminology used in this book, and can not be made so, being applied to different parts of the wing by writers on different orders of insects. They are included here as they are frequently used, as a matter of convenience, by those who have adopted the uniform terminology. The discal cell of the Lepidoptera is cell $R+M+1stM_2$; that of the Diptera is cell 1st M_2; and that of the Trichoptera is cell R_{2+3}.

The anal area and the preanal area of the wing.—In descriptions of wings it is frequently necessary to refer to that part of the wing supported by the anal veins; this is designated as the *anal area* of the wing; and that part lying in front of the anal area, including all of the wing except the anal area, is termed the *preanal area*.

IV. THE ABDOMEN

a. THE SEGMENTS OF THE ABDOMEN

The third and terminal region of the body, the abdomen, consists of a series of approximately similar segments, which as a rule are without appendages excepting certain segments near the caudal end of the body.

The body-wall of an abdominal segment is usually comparatively simple, consisting in adults of a tergum and a sternum, united by lateral conjunctivæ. Sometimes there are one or two small sclerites on each lateral aspect of a segment; these are probably reduced pleura.

The number of segments of which the abdomen appears to be composed varies greatly in different insects. In the cuckoo-flies (Chrysididæ) there are usually only three or four visible; while in many insects ten or eleven can be distinguished. All intergrades between these extremes occur.

The apparent variation in the number of abdominal segments is due to two causes: in some cases, some of the segments are telescoped; and in others, adjacent segments coalesce, so that two or more segments appear as one.

A study of embryos of insects has shown that the abdomen consists typically of eleven segments; although this number may be reduced during the development of the insect by the coalescence of adjacent segments.

In some insects there is what appears to be a segment caudad of the eleventh segment; this is termed the *telson*. The telson differs from the segments preceding it in that it never bears appendages.

Special terms have been applied, especially by writers on the Coleoptera, to the caudal segments of the abdomen. Thus the terminal segment of a beetle's abdomen when exposed beyond the elytra is termed the *pygídium;* the tergite cephalad of the pygidium, especially in beetles with short elytra, the *propygídium;* and the last abdominal sternite, the *hypopy̆gium*. The term hypopygium is also applied to the genitalia of male Diptera by writers on that order of insects.

b. THE APPENDAGES OF THE ABDOMEN

In the early embryonic stages of insects, each segment of the abdomen, except the telson, bears a pair of appendages (Fig. 89). This indicates that the primitive ancestor of insects possessed many legs, like a centipede. But the appendages of the first seven abdominal segments are usually lost during embryonic life, these segments being without appendages in postembryonic stages, except in certain Thysanura and Collembola, and in some larvæ.

Fig. 89.-Embryo of *Hydrophilus* showing abdominal appendages.

Reference is made here merely to the primary appendages of the segments, those that are homodynamous with the thoracic legs; secondarily developed appendages, as for example, the tracheal gills, are present in the immature instars of many insects.

The styli or vestigial legs of certain Thysanura.—In certain Thysanura the coxa of each middle and hind thoracic leg bears a small appendage, the *stylus* (Fig. 90); and on from one to nine abdominal segments there is a pair of similar styli. These abdominal styli are believed to be homodynamous with those of the thoracic legs, and must, therefore, be regarded as vestiges of abdominal legs.

The collophore of the Collembola.—Although in the postembryonic stages of Collembola the collophore is an unpaired organ on the middle line of the ventral aspect of the first abdominal segment, the fact that it arises in the embryo as a pair of appendages comparable in position to the thoracic legs, has led to the belief that it represents the legs of this segment. The structure of the collophore is described more fully later in the chapter treating of the Collembola.

The spring of the Collembola.—The spring of the Collembola, like the collophore, is believed to represent a pair of primary appendages. This organ is discussed in the chapter treating of the Collembola.

The genitalia.—In most insects there are more or less prominent appendages connected with the reproductive organs. These appendages constitute in males the *genital claspers* and in females the *ovipositor;* to them have been applied the general term *genitālia,* they are also known as the *gonapŏphyses.*

The genitalia, when all are developed consist of three pairs of appendages. Writers vary greatly in their views regarding the seg-

ments of the abdomen to which these appendages belong. One cause of difference is that some writers regard the last segment of the abdomen as the tenth abdominal segment while others believe it to be the eleventh. This segment bears the cerci when they are present. The genitalia are borne either by the two or the three segments immediately preceding the last. If the last segment is the eleventh the genitalia are, according to one view, the appendages of the eighth, ninth, and tenth segments; according to another view, they are the appendages of the ninth and tenth segments, those of the tenth segment being doubled.

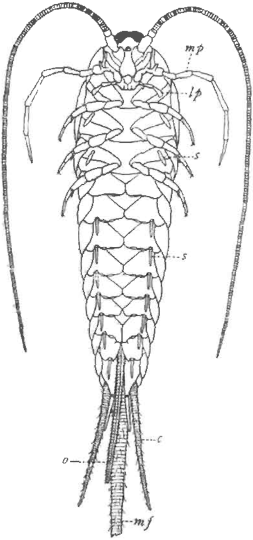

Fig. 90.—Ventral aspect of Machilis; *c*, cercus: *lp*, labial palpus; *mf*, median caudal filament; *mp*, maxillary palpus; *o*, ovipositor; *s*, *s*, styli. That part of the figure representing the abdomen is after Oudemans.

The genitalia of many insects have been carefully figured and described and special terms have been applied to each of the parts. But as most of these descriptions have been based upon studies of representatives of a single order of insects or even of some smaller group, there is a great lack of uniformity in the terms applied to homologous parts in the different orders of insects; such of these terms as are commonly used are defined later in the characterizations of the several orders of insects.

The cerci.—In many insects there is a pair of caudal appendages which are known as the *cerci;* these are the appendages of the eleventh abdominal segment, the last segment of the body except in the few cases where a telson is present.

The cerci vary greatly in form; in some insects, as in most Thysanura, in the Plecoptera, and in the Ephermerida, they are long and

many jointed; while in others they are short and not segmented The function of the cerci is different in different insects; they are believed to be tactile in some, olfactory in others and in some males they aid in holding the femal during copulation.

Fig. 91.—*Lepisma saccharina.*

The median caudal filament.—In many of th Ephemerida and in some of the Thysanura, the las abdominal segment bears a long, median filamen which resembles the many-jointed cerci of thes insects (Fig. 91); this filament is believed to be prolongation of the tergum of this segment and not true appendage like the cerci.

The prolegs of larvæ.—The question whether th prolegs of larvæ represent true appendages or a merely hypodermal outgrowths has been much di cussed. Several embryologists have shown that embryos of Lepidoptera and of saw-flies limb-rud ments appear on all or most of the abdominal se ments; and that they very soon disappear on tho segments which in the larva have no legs while on other segmen they are transferred into functional prolegs. If this view is esta lished we must regard such prolegs as representing primitive abd minal appendages, that is as true abdominal legs.

V. THE MUSIC AND THE MUSICAL ORGANS OF INSECTS

Much has been written about music; but the greater part of t literature refers to music made by man for human ears. Man, ho ever, is only one of many musical animals; and, although he exc all others in musical accomplishments, a study of what is done by humbler relatives is not without interest.

The songs of birds command the attention of all observers. E there is a great orchestra which is performing constantly through warmer portions of the year, which is almost unnoticed by m Occasionally there is a performer that cannot be ignored, as:—

> "The shy Cicada, whose noon-voice rings
> So piercing shrill that it almost stings
> The sense of hearing." (ELIZABETH AKERS.)

But the great majority fiddle or drum away unnoticed by human e

Musical sounds are produced by many different insects, and in various ways. These sounds are commonly referred to as the songs of insects; but properly speaking few if any insects sing; for, with some possible exceptions, the note of an insect is always at one pitch, lacking musical modulations like those of the songs of man and of birds.

The sound produced by an insect may be a prolonged note, or it may consist of a series of short notes of varying length, with intervals of rest of varying lengths. These variations with differences in pitch give the wide range of insect calls that exists.

In some cicadas where the chambers containing the musical organs are covered by opercula, the insect can give its call a rhythmic increase and decrease of loudness, by opening and closing these chambers.

As most insect calls are strident, organs specialized for the production of these calls are commonly known as stridulating organs. But many sounds of insects are produced without the aid of organs specialized for the production of sound. The various ways in which insects produce sounds can be grouped under the following heads:

First.—By striking blows with some part of the body upon surrounding objects.

Second.—By rapid movements of the wings. In this way is produced what may be termed the music of flight.

Third.—By rasping one hard part of the body upon another. Under this head fall the greater number of stridulating organs.

Fourth.—By the rapid vibration of a membrane moved by a muscle attached to it. This is the type found in the cicadas.

Fifth.—By the vibration of membranes set in motion by the rush of air through spiracles. The reality of this method has been questioned.

Sixth.—By rapid changes of the outline of the thorax due to the action of the wing muscles.

a SOUNDS PRODUCED BY STRIKING OBJECTS OUTSIDE THE BODY

Although the sounds produced by insects by striking blows with some part of the body upon surrounding objects are not rapid enough to give a musical note, they are referred to here for the sake of completeness.

The most familiar sounds of this kind are those produced by the insects known as the death-watch. These are small beetles of the family Ptinidæ, and especially those of the genus *Anobium*. These are wood-boring insects, frequently found in the woodwork of old

houses and in furniture, where they make a ticking sound by striking their heads against the walls of their burrows. The sound consists of several, sharp, distinct ticks, followed by an interval of silence, and is believed to be a sexual call.

The name death-watch was applied to these insects by superstitious people who believed that it presaged the death of some person in the house where it is heard. This belief probably arose from the fact that the sound is most likely to be heard in the quiet of the night, and would consequently be observed by watchers by sick-beds.

The name death-watch has also been applied to some species of the Psocidæ, *Clothilla pulsatoria* and *Atropos divinatoria*, which have been believed to make a ticking sound. This, however, is doubted by some writers, who urge that it is difficult to believe that such minute and soft insects can produce sounds audible to human ears.

The death-watches produce their sounds individually; but an interesting example of an insect chorus is cited by Sharp ('99, p. 156), who, quoting a Mr. Peal, states that an ant, presumably an Assamese species, "makes a concerted noise loud enough to be heard by a human being at twenty or thirty feet distance, the sound being produced by each ant scraping the horny apex of the abdomen three times in rapid succession on the dry, crisp leaves of which the nest is usually composed."

b. THE MUSIC OF FLIGHT

The most obvious method by which insects produce sounds is by beating the air with their wings during flight. It can be readily seen that if the wing-strokes are sufficiently rapid and are uniform, they will produce, like the flapping reeds of a mouth organ, a musical note.

When, however, we take into account the fact that to produce the lowest note regularly employed in music, the C of the lowest octave, requires 32 vibrations a second, *i. e.*, nearly 2,000 vibrations per minute, it will seem marvellous that muscular action can be rapid enough to produce musical notes. Nevertheless, it is a fact that many insects sing in this way; and too their notes are not confined to the lower octaves. For example, the common house fly hums F of the middle octave, to produce which, it must vibrate its wings 345 times per second or 20,700 times per minute.

As a rule, the note produced by the wings is constant in each species of insect. Still with insects, as with us, the physical condition of the singer has its influence. The vigorous honey-bee makes the A of 435 vibrations, while the tired one hums on the E of 326 vibrations.

In each of these families the vibrating element of the stridulating organ is a portion of one or of both of the fore wings; but this is set in motion in several different ways. In some exotic Acridiidæ abdominal stridulating organs exist.

The stridulating organs of the Acridiidæ.—With many species of the Acridiidæ we find the males furnished with stridulating organs; but these are comparatively simple, and are used only in the day time.

Two methods of stridulation are used by members of this family. The simpler of these two methods is employed by several common species belonging to the Œdipodinæ; one of which is the Carolina locust, *Dissosteira carolina*, whose crackling flight is a common feature of country roadsides. These locusts, as they fly, rub the upper surface of the costal margin of the hind wings upon the lower surface of the thickened veins of the fore wings, and thus produce a loud but not musical sound.

The second method of stridulation practiced by locusts consists in rubbing the inner surface of the hind femora, upon each of which there is a series of bead-like prominences (Fig. 92), against the outer surface of the fore wings. With these insects, there is a thickening of the radius in the basal third of each fore wing, and a widening of the two areas between this vein and the costal margin of the wing, which serves as a sounding board (Fig. 93). The two wings and femora constitute a pair of violin-like organs; the thickened radius in each case corresponding to the strings; the membrane of the wing, to the body of the instrument; and the file of the femur, to the bow. These two organs are used simultaneously. When about to stridulate, the insect

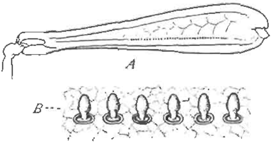

Fig. 92.—A, hind femora of *Stenobothrus*, B, file greatly enlarged.

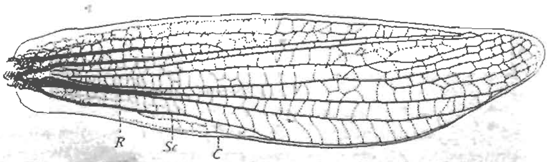

Fig. 93.—Fore wing of a male of *Stenobothrus*. R, radius; *Sc*, subcosta; *C*, costa.

places itself in a nearly horizontal position, and raising both hind legs at once rasps the femora against the outer surface of the wings. The most common representatives of insects that stridulate in this way belong to the genus *Stenobothrus*.

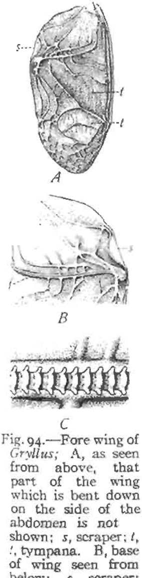

Fig. 94.—Fore wing of *Gryllus;* A, as seen from above, that part of the wing which is bent down on the side of the abdomen is not shown; *s*, scraper; *t*, *t*, tympana. B, base of wing seen from below; *s*, scraper; *f*, file. C, file greatly enlarged.

The stridulating organs of the Gryllidæ and the Locustidæ.—The stridulating organs of the Gryllidæ and the Locustidæ are of the same type, and are the most highly specialized found in the Orthoptera. They consist of modified portions of the fore wings; both the vibrating and the rasping elements of the organs pertaining to the wings.

It is by rubbing the two fore wings together that sound is produced.

In what is probably the more generalized condition of the organs, as seen in *Gryllus*, each fore wing bears a rasping organ, the file (Fig. 94, *f*) a hardened area, the *scraper* (Fig. 94, *s*), against which the file of the other wing acts, and vibrating areas, the *tympana* (Fig. 94, *t*, *t*). As the file of either wing can be used to set the tympana of the wings in vibration, we may say that *Gryllus* is ambidextrous.

When the cricket wishes to make his call, he elevates his fore wings so that they make an angle of about forty-five degrees with the body; then holding them in such a position that the scraper of one rests on the file of the other, he moves the wings back and forth laterally, so that the file and scraper rasp upon each other. This throws the wings into vibration and produces the call.

It is easy to observe the chirping of crickets. If one will move slowly towards a cricket that is making his call, and stop when the cricket stops chirping until he gains confidence and begins again, one can get sufficiently near to see the operation clearly. This can be done either in the day time or at night with the aid of a light.

The songs of the different genera of crickets can be easily distinguished, and that of each species, with more care. Writers on the Orthoptera have carefully described the songs of our more common crickets, and especially those of the tree crickets. The rate of chirping

is often influenced by temperature, being slower in cool nights than in warm ones; and becoming slower towards morning if the temperature falls.

In certain genera of crickets as *Nemobius* and *Œcanthus*, while each fore wing is furnished with a file and tympana, the scraper of the right wing is poorly formed and evidently not functional. As these insects use only the file of the right wing to set the tympana of the wings in vibration, they may be said to be right-handed.

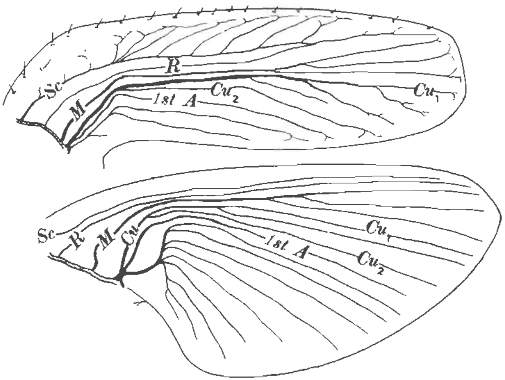

Fig. 95.—Wings of a female nymph of *Œcanthus* (From Comstock and Needham).

In the Locustidæ a similar modification of the function of the stridulating organs has taken place. In all of our common representatives of the family, at least, only one of the files is used. But in these cases it is the file of the left wing that is functional; we may say, therefore, that so far as observed the Locustidæ are left-handed. Different genera exhibit great differences as to the extent of the reduction of the unused parts of the stridulating organs. The file is present in both wings of all of the forms that I have studied; but the unused file is sometimes in a vestigial condition. The scraper is less persistent, being frequently entirely lacking in one of the wings. In some cases, the tympana of one wing have been lost; but in others the tympana of both wings are well preserved, although only one file

is used. In these cases it is probable that the tympana of both wings are set in vibration by the action of the single functional file.

The determination of the homologies of the parts of the wing that enter into the composition of the stridulating organs was accomplished by a study of the tracheation of the wings of nymphs (Comstock and Needham, '98–'99). The results obtained by a study of the wings of *Œcanthus* will serve as an illustration.

Figure 95 represents the wings of a female nymph of this genus, with the tracheæ lettered. The only parts to which we need to give attention in this discussion are the cubital and anal areas of the fore wing; for it is this part of the wing that is modified in the male to form the musical organ. Both branches of cubitus are present, and Cu_1 bears three accessory branches. The three anal tracheæ are present and are quite simple.

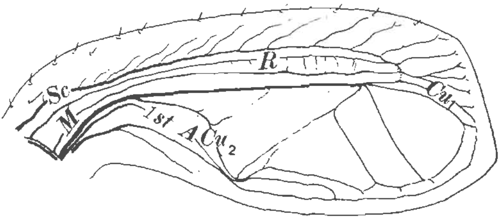

Fig. 96.—Fore wing of a male nymph of *Œcanthus* (From Comstock and Needham).

The homologies of the tracheæ of the fore wing of a male nymph, Figure 96, were easily determined by a comparison with the tracheæ of the female. The most striking difference between the two sexes is a great expanding of the area between the two branches of cubitus in the male, brought about by the bending back of the basal part of Cu_2.

The next step in this study was to compare the wing of an adult male, Figure 97, with that of the nymph of the same sex; and the solution of the problem was soon reached. It can be easily seen that the file is on that part of Cu_2 that is bent back toward the inner margin of the wing (Fig. 97, *f*); the tympana are formed between the branches of cubitus (Fig. 97, *t, t*); and the scraper is formed at the outer end of the anal area (Fig. 97, *s*).

A similar study was made of the wings of *Conocephalus*, as an example of the Locustidæ. Figure 98 represents the wings of a male nymph; and Figure 99 the fore wing of an adult. The most striking feature, and one characteristic of the family, is tha the musica organ occupie an area nea the base (the wing whic is small compared wit the area occupied by the musical organs of the Gryllidæ. Bu here, as in the Gryllidæ, the file is borne by the basal part of Cu_2, th

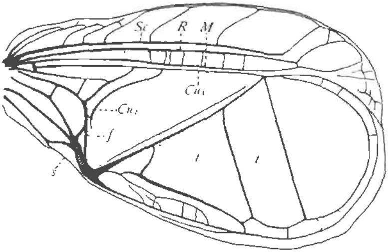

Fig. 97.—Fore wing of an adult male of *Œcanthus*; *f*, vein bearing the file; *s*, scraper; *t*, *t*, tympana.

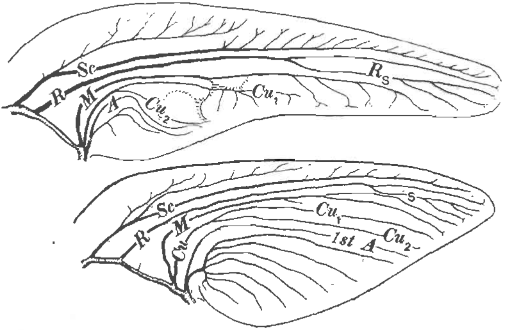

Fig. 98.—Wings of a male nymph of *Conocephalus*, (From Comstock and Needham).

tympana are formed between the branches of cubitus, and the scrap is formed at the outer end of the anal area.

Rasping organs of other than orthopterous insects.—Rasping organs are found in many other than orthopterous insects and vary

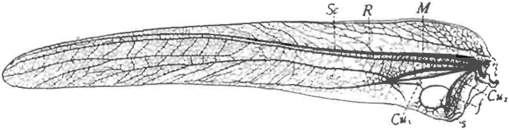

Fig. 99.—Right fore wing of an adult male of *Conocephalus*, seen from below; *f*, file; *s*, scraper.

greatly in form and in their location on the body. Lack of space forbids any attempt to enumerate these variations here; but examples of various types of stridulating organs will be described in later chapters when treating of the insects that possess them. As in the Orthoptera, they consist of a rasp and a scraper. The rasp is a file-like area of the surface of a segment of the body or of an appendage; and the scraper is a hard ridge or point so situated that it can be drawn across the rasp by movements of the body or of an appendage. In some cases the apparatus consists of two rasps so situated that they can be rubbed together.

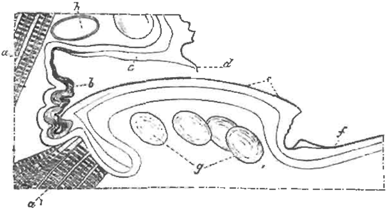

Fig. 100.—Stridulating organ of an ant, *Myrmica rubra* (From Sharp after Janet): *d*, scraper; *e*, file.

With many beetles one of the two parts of the stridulating organ is situated upon the elytra; and it is quite probable that in these cases the elytra acts as vibrating surfaces, as do the wings of locusts and crickets. But in many cases as where a part of a leg is rubbed against a portion of a thoracic segment, there appears to be no vibrating surface unless it is the wall of the body or of the appendage that acts as a sounding board. In the stridulating organ of *Myrmica rubra*, var. *lævinodis*, figured by Janet (Fig. 100), the scraper is the posterior border of one abdominal segment, and the file is situated on the dorsum of the following segment. It is quite conceivable that in this case

the dorsal wall of the segment bearing the file is made to vibrate by the successive impacts of the scraper upon the ridges of the file. In fact this seems to me more probable than that the sound produced is merely that of the scraper striking against the successive ridges of the file. There is at least one recorded case where the body wall is specialized to act as a sounding board. According to Sharp ('95, p. 200), in the males of the Pneumorides, a tribe of South African Acridiidæ, where the phonetic organ is situated on the abdomen, this part is inflated and tense, no doubt with the result of increasing the volume and quality of the sound.

Ordinarily the stridulating organs of insects are fitted to produce notes of a single degree of pitch; but Gahan ('00) figures those of some beetles that are evidently fitted to produce sounds of more than one degree of pitch; the file of *Hispopria foveicollis*, consists of three parts, one very finely striated, followed by one in which the striæ are much coarser, and this in turn followed by one in which the striation is intermediate in character between the other two.

While the stridulating organs of the Orthoptera are possessed almost exclusively by the males, in the Coleoptera, very many species of which stridulate, the phonetic organs are very commonly possessed by both sexes, and serve as a mutual call. In one genus of beetles, *Phonapate*, stridulating organs have been found only in the females (Gahan, '00).

It seems evident that in the great majority of cases the sounds produced by insects are sexual calls; but this is not always so. It was pointed out long ago by Charles Darwin that "beetles stridulate under various emotions, in the same manner as birds use their voices for many purposes besides singing to their mates. The great *Chiasognathus* stridulates in anger or defiance; many species do the same from distress or fear, if held so that they cannot escape; by striking the hollow stems of trees in the Canary Islands, Messrs. Wollaston and Crotch were able to discover the presence of beetles belonging to the genus *Acalles* by their stridulation. Lastly the male *Ateuchus* stridulates to encourage the female in her work and from distress when she is removed" (*The Descent of Man*).

The most remarkable case where stridulating organs have been developed for other than sexual purposes is that of the larvæ of certain Lucanidæ and Scarabæidæ described by Schiodte ('74). In these larvæ there is a file on the coxa of each middle leg, and the hind legs are shortened and modified so as to act as scrapers. The most highly

specialized example of this type of stridulating organ is possessed by the larvæ of *Passalus*, in which the legs of the third pair are so much shortened that the larvæ appear to have only four legs; each hind leg is a paw-like structure fitted for rasping the file (Fig. 101).

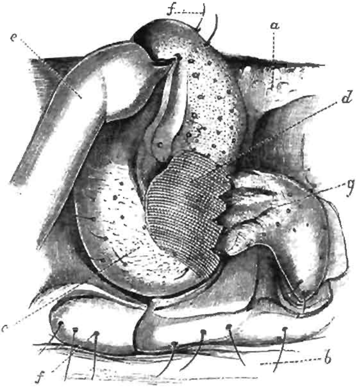

Fig. 101.—Stridulating organ of a larva of *Passalus*; *a*, *b*, portions of the metathorax; *c*, coxa of the second leg; *d*, file; *e*, basal part of femur of middle leg; *f*, hairs with chitinous process at base of each; *g*, the diminutive third leg modified for scratching the file (From Sharp).

No satisfactory explanation of the advantage to these larvæ of the possession of stridulating organs has been offered; we can only say that the sound produced by them is obviously not a sexual call.

d. THE MUSICAL ORGANS OF A CICADA

With the cicadas there exists a type of stridulating organ peculiar to them, and one that is the most complicated organ of sound found in the animal kingdom. Yet, while the cicadas are the most noisy of the insect world, the results obtained by their complicated musical apparatus are not comparable with those produced by the comparatively simple vocal organs of birds and of man.

It is said that in some species of *Cicada* both sexes stridulate; but as a rule the females are mute, possessing only vestiges of the musical apparatus.

The structure of the stridulating organs varies somewhat in details in different species of Cicada; but those of *Cicada plebeia*, which were described and figured by Carlet ('77), may be taken as an example of the more perfect form. In the male of this species there is a pair of large plates, on the ventral side of the body, that extend back

from the hind border of the thorax and overlap the basal part of the abdomen; these are the *opercula* (Fig. 102, *o*). The opercula are expansions of the sternellum of the metathorax, and each serves as a lid covering a pair of cavities, containing the external parts of the musical apparatus of one side of the body.

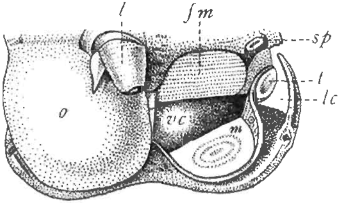

Fig. 102.—The musical apparatus of a cicada: *fm*, folded membrane; *l*, base of leg; *lc*, lateral cavity; *m*, mirror; *o*, operculum, that of the opposite side removed; *sp*, spiracle; *t*, timbal; *vc*, ventral cavity (After Carlet).

The two cavities covered by a single operculum may be designated as the *ventral cavity* (Fig. 102, *v. c.*) and the *lateral cavity* (Fig. 102, *l. c.*) respectively. Each cavity is formed by an infolding of the body-wall.

In the walls of these cavities are three membranous areas; these are known as the *timbal*, the *folded membrane*, and the *mirror*.

The timbal is in the lateral cavity on the lateral wall of the partition separating the two cavities (Fig. 102, *t*); the other two membranes are in the ventral cavity. The folded membrane is in the anterior wall of the ventral cavity (Fig. 102, *f. m.*); and the mirror is in the posterior wall of the same cavity (Fig. 102, *m*). Within the body, there is in the region of the musical apparatus a large thoraco-abdominal air chamber, which communicates with the exterior through a pair of spiracles (Fig. 102, *sp*); and a large muscle, which extends from the furca of the second abdominal segment to the inner face of the timbal.

By the contraction of this muscle the timbal is pulled towards the center of the body; and when the muscle is relaxed, the elasticity of the chitinous ring supporting the timbal causes it to regain its former position. By a very rapid repetition of these movements of the timbal the sound is produced.

It is probable that the vibrations of the timbal are transmitted to the folded membrane and to the mirror by the air contained in the large air chamber mentioned above; as the strings of a piano are made to vibrate by the notes of a near-by violin. The sound, however, is produced primarily by the timbal, the destruction of which

renders the insect a mute; while the destruction of the other membranes, the timbal remaining intact, simply reduces the sound.

The chief function of the opercula is doubtless the protecting of the delicate parts of the musical organ; but as they can be lifted slightly and as the abdomen can be moved away from them to some extent, the chambers containing the vibrating parts of the organ can be opened and closed, thus giving a rhythmic increase and decrease of the loudness of the call.

e. THE SPIRACULAR MUSICAL ORGANS

There has been much discussion of the question whether insects, and especially Diptera and Hymenoptera, possess a sound-producing organ connected with the spiracles or not. Landois ('67) believed that he found such an organ and figures and describes it in several insects. It varies greatly in form in different insects. In the Diptera it consists of a series of leaf-like folds of the intima of the trachea; these are held against each other by a special humming ring, which lies close under the opening of the spiracle; and is found within two or all four of the thoracic spiracles. These membranous folds of the intima are set in vibration by the rush of air through the spiracles.

In the May-beetle, according to Landois, a buzzing organ is found near each of the fourteen abdominal spiracles. It is a tongue-like fold projecting into the lumen of the trachea under the base of the closing apparatus. On its upper surface it is marked with very fine arched furrows. He concludes that this tongue is put in vibration by the breathing of the insect, and hence the buzzing of the flying beetle.

If insects produce sounds in the way described by Landois, they have a voice quite analogous to our own. But the validity of the conclusions of Landois has been seriously questioned; the subject, therefore, demands further investigation.

f. THE ACUTE BUZZING OF FLIES AND BEES

Many observers have found that when the wings of a fly or of a bee are removed or held so that they can not vibrate the insect can still produce a sound. The sound produced under these circumstances is higher, usually an octave higher, than that produced by the wings. It is evident, therefore, that these insects can produce sounds in two ways; and an extended search has been made for the organ or organs producing the higher note.

Landois believed that the spiracular organs referred to above wer the source of the acute sound. But more recently Pérez ('78) an Bellesme ('78) have shown that when the spiracles are closed artifi cially the insect can still produce the high tone. Pérez attributes th sound to the vibrations of the stumps of the wings against the soli parts which surround them or of the sclerites of the base of the win against each other. But Bellesme maintains that the sound is pro duced by changes in the form of the thorax due to the action of th wing-muscles.* When the wing-muscles are at rest the section of thi region, according to this writer, represent an ellipse elongated ve tically; the contraction of the muscles transforms it to an ellips elongated laterally; the thorax, therefore, constitutes a vibratin body which moves the air like a tine of a tuning fork. Bellesm states that by fastening a style to the dorsal wall of the thorax h obtained a record of the rate of its vibrations, the number of whic corresponded exactly to that required to produce the acute soun which the ear perceives.

The fact that the note produced when the wings are removed i higher than that produced by the wings is supposed by Bellesme to b due to the absence of the resistance of air against the wings, whic admits of the maximum rate of contraction of the wing-muscles.

g. MUSICAL NOTATION OF THE SONGS OF INSECTS

Mr. S. H. Scudder ('93) devised a musical notation by which th songs of stridulating insects can be recorded. As the notes are alway at one pitch the staff in this notation consists of a single horizonta line, the pitch being indicated by a separate statement. Each ba represents a second of time, and is occupied by the equivalent of a semibreve; consequently a quarter note ♩, or a quarter rest 𝄽, repre sents a quarter of a second; a sixteenth note 𝅘𝅥𝅯, or a sixteenth rest a sixteenth of a second and so on. For convenience's sake he intro duced a new form of rest, shown in the second example given below which indicates silence through the remainder of a measure; thi differs from the whole rest commonly employed in musical notatio by being cut off obliquely at one end.

*This view was maintained by Siebold at a much earlier date in his *Anatom of the Invertebrates.*

The following examples taken from his paper on "The Songs of our Grasshoppers and Crickets" will serve to illustrate this method of notation.

The chirp of *Gryllotalpa borealis* (Fig. 103) "is a guttural sort of sound, like grü or grēēu, repeated in a trill indefinitely, but seldom

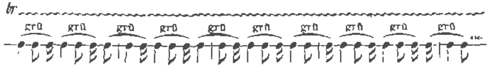

Fig. 103.—The chirp of *Gryllotalpa borealis* (From Scudder).

for more than two or three minutes, and often for less time. It is pitched at two octaves above middle C."

Fig. 104.—The chirp of the katydid (From Scudder).

The note of the true katydid, *Cyrtophyllus concavus*, (Fig. 104) "which sounds like *xr*, has a shocking lack of melody; the poets who have sung its praises must have heard it at a distance that lends enchantment." "They ordinarily call 'Katy' or say 'She did' rather than 'Katy did'; that is they rasp their fore wings twice more frequently than thrice." Mr. Scudder in his account of this song fails to indicate its pitch.

h. INSECT CHORUSES

Most insect singers are soloists, singing without reference to other singers or in rivalry with them. But there are a few species the members of which sing in unison with others of their kind that are near them. The most familiar sound of autumn evenings in rural places in this country is a chorus of the snowy tree cricket, *Œcanthus niveus*. Very many individuals of this species, in fact all that are chirping in any locality, chirp in unison. Early in the evening, when the chirping first begins, there may be a lack of unanimity in keeping time; but this lasts only for a short period, soon all chirp in unison, and the monotonous beat of their call is kept up uninterrupted throughout the night. Individual singers will stop to rest, but when they start again they keep time with those that have continued the chorus.

Other instances of insect choruses have been recorded. Sharp ('99, 156) quotes accounts of two produced by ants; one of these is given on an earlier page (p. 80).

CHAPTER III

THE INTERNAL ANATOMY OF INSECTS

BEFORE making a more detailed study of the internal anatomy of insects, it is well to take a glance at the relative positions of the different systems of organs within the body of insects and other arthropods.

One of the most striking features in the structure of these animals is that the body-wall serves as a skeleton, being hard, and giving support to the other organs of the body. This skeleton may be represented, therefore, as a hollow cylinder. We have now to consider the arrangement and the general form of the organs contained in this cylinder.

The accompanying diagram (Fig. 105), which represents a vertical, longitudinal section of the body, will enable the student to gain an

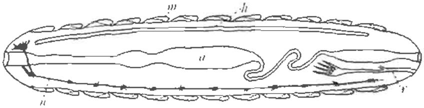

Fig. 105.—Diagram showing the relations of the internal organs; *a*, alimentary canal; *h*, heart; *m*, muscle; *n*, nervous system; *r*, reproductive organs.

idea of the relative positions of some of the more important organs. The parts shown in the diagram are as follows: The body-wall, or skeleton; this is made up of a series of overlapping segments; that part of it between the segments is not hardened with chitine, thus remaining flexible and allowing for the movements of the body. Just within the body-wall, and attached to it, are represented a few of the muscles (*m*); it will be seen that these muscles are so arranged that the contraction of those on the lower side of the body would bend it down while the contraction of those on the opposite side would act in the opposite direction, other muscles not shown in the figure provide for movements in other directions. The alimentary canal (*a*) occupies the centre of the body, and extends from one end to the other. The heart (*h*) is a tube open at both ends, and lying between the alimentary canal and the muscles of the back. The central part of the nervous system (*n*) is a series of small masses of nervous matter connected by

two longitudinal cords: one of these masses, the brain, lies in the head above the alimentary canal; the others are situated, one in each segment, between the alimentary canal and the layer of muscles of the ventral side of the body; the two cords connecting these masses, or ganglia, pass one on each side of the oesophagus to the brain. The reproductive organs (*r*) lie in the cavity of the abdomen and open near the caudal end of the body. The respiratory organs are omitted from this diagram for the sake of simplicity. We will now pass to a more detailed study of the different systems of organs.

I. THE HYPODERMAL STRUCTURES

The active living part of the body-wall is the hypodermis, already described in the discussion of the external anatomy of insects. In addition to the external skeleton, there are derived from the hypodermis an internal skeleton and several types of glands.

a. THE INTERNAL SKELETON

Although the skeleton of an insect is chiefly an external one, there are prolongations of it extending into the body-cavity. These inwardly directed processes, which serve for the attachment of muscles and for the support of other viscera are termed collectively the *internal skeleton* or *endo-skeleton*. The internal skeleton is much more highly developed in adult insects than it is in the immature instars.

Sources of the internal skeleton.—The parts of the internal skeleton are formed in two ways: first by the chitinization of tendons of muscles; and second, by invaginations of the body-wall.

Chitinized tendons.—Chitinized tendons of the muscles that move the mouth-parts, of muscles that move the legs, and of other muscles are of frequent occurrence. As these chitinized tendons help support the internal organs they are considered as a part of the internal skeleton.

Invaginations of the body-wall or apodemes.—The second and more important source of the parts of the internal skeleton consists of invaginations of the body-wall. Such an invagination is termed an *apodeme*. The more important apodemes, if not all, arise as invaginations of the body-wall between sclerites or at the edge of a sclerite on the margin of a body-segment; although by the fusion of sclerites about an apodeme, it may appear to arise from the disc of a sclerite.

Frequently, in the more generalized insects, the mouth of an apodeme remains open in the adult insects. In Figure 106 are represented two apodemes that exist in the thorax of a locust, *Melanoplus*. Each of these (*ap* and *ap*) is an invagination of the body-wall, between the episternum and the epimeron of a segment, immediately above the base of a leg. These are known as the lateral apodemes of the thorax and serve as points of attachment of muscles.

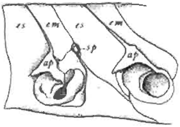

Fig. 106.—Ental surface of the pleurites of the meso- and metathorax of *Melanoplus*, showing the lateral apodemes, *ap*, *ap*.

The number of apodemes may be very large, and it varies greatly in different insects. Among the more important apodemes are the following:—

The tentorium.—The chief part of the internal skeleton of the head is termed the *tentorium*. This was studied by Comstock and Kochi ('02). We found that in the generalized insects studied by us it is composed of two or three pairs of apodemes that, extending far into the head, meet and coalesce. The three pairs of apodemes that may enter into the formation of the tentorium were termed the *anterior*, the *posterior*, and the *dorsal arms of the tentorium* respectively. The coalesced and more or less expanded tips of these apodemes constitute the *body of the tentorium*. From the body of the tentorium there extend a variable number of processes or chitinized tendons.

The posterior arms of the tentorium.—The posterior arms of the tentorium (Fig. 107, 109, 110, *pt*) are the lateral apodemes of the

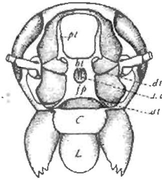

Fig. 107.— Tentorium of a cockroach, dorsal aspect.

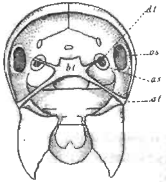

Fig. 108.—Part of the tentorium of a cricket, ventral aspect.

maxillary segment. In many Orthoptera the open mouth of the apodeme can be seen on the lateral aspect of the head, just above the

articulation of the maxilla (Fig. 48). In the Acridiidæ (Fig. 109) these apodemes bear a striking resemblance to the lateral apodemes of the thorax (Fig. 106), except that the ventral process of the maxillary apodeme is much more prominent, and the two from the opposite sides of the head meet and coalesce, thus forming the caudal part of the body of the tentorium.

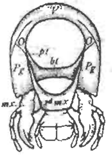

Fig. 109.—Head of *Melanoplus*, caudal aspect.

The anterior arms of the tentorium.—Each anterior arm of the tentorium (Fig. 107, 108, 110, *at*) is an invagination of the body-wall which opens on the margin of the antecoxal piece of the mandible when it is distinct; if this part is not distinct the apodeme opens between the clypeus and the front (Fig. 46, *at*).

The dorsal arms of the tentorium.—Each dorsal arm of the tentorium arises from the side of the body of the tentorium between the anterior and posterior arms and extends either to the front or to the margin of the antennal sclerite (Fig. 107, 108, 110, *dt*).

The frontal plate of the tentorium.—In the cockroaches the anterior arms of the tentorium meet and fuse, forming a broad plate situated between the crura cerebri and the mouth; this plate was termed by us the *frontal plate of the tentorium* (Fig. 107, *fp*). On each side, an extension of this plate connects it with the body of the tentorium; these enclose a circular opening through which pass the crura cerebri.

Other cervical apodemes and some chitinized tendons are described in the paper cited above.

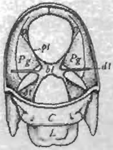

Fig. 110.—Tentorium of *Melanoplus*, cephalic aspect. The distal end of the dorsal arms detached.

The endothorax.—The internal skeleton of the thorax is commonly termed the *endothorax;* under this head are not included the internal processes of the appendages.

The endothorax is composed of invaginations of each of the sections of a thoracic ring. Those portions that are derived from tergites are termed *phragmas;* those derived from the pleurites, *lateral apodemes;* and those, from the sternites, *furcæ.*

The phragmas.—A phragma is a transverse partition extending entad from the front or the hind margin of a tergite; three of them are commonly recognized; these were designated by Kirby and Spence (1826) the *prophragma*, the *mesophragma*, and the *metaphragma;* but, as they do not arise one from each segment of the

thorax, and arise differently in different insects, these terms are mis leading. No phragma is borne by the prothorax; the mesothorax may bear two and the metathorax one, or the mesothorax one and the metathorax two. A more definit terminology is that used by Snodgrass ('09) by which the anterio phragma of any segment is terme the *prephragma* of that segment and the posterior phragma of an segment is termed the *postphragm* of that segment.

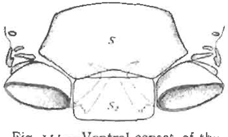

Fig. 111.—Ventral aspect of the metathorax of *Stenopelmatus*. The position of the furca within the body is represented by a dotted line.

The lateral apodemes.—Each lateral apodeme is an invagination o the body-wall between the episternum and the epimeron. The lateral apodemes are referred to abov (Fig. 106).

The furcæ.—Each furca is an invagination of the body-wall arisin between the sternum and the sternellum (Fig. 111); when the sternellum is obsolete, as it is in most insects, the furca arises at the cauda margin of the segment (Fig. 112).

b. THE HYPODERMAL GLANDS

A gland is an organ that possesses the function of either trans forming nutritive substances, which it derives from the blood, int some useful substance, as mucus, wax, or venom, or of assimilatin and removing from the body waste material.

The different glands vary greatly in structure; many are *unicellular*, the gland consisting of a single cell, which differs from the other cells of the epithelium of which it is a part in being larger and in possessing the secreting and excreting functions; others are *multicellular*, consisting of more than one cell, usually of many cells. In these cases the glandular area usually becomes invaginated, and provided with an efferent duct; and often the invagination is much branched.

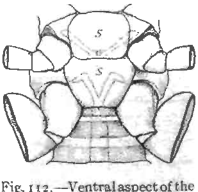

Fig. 112.—Ventral aspect of the meso—and metathorax of *Gryllus*; the positions of the furcæ within the body are indicated by dotted lines.

The glands found in the body of an insect can be grouped unde three heads; the hypodermal glands, the glands of the alimentary

canal, and the glands of the reproductive organs. In this place reference is made only to the hypodermal glands, those developed from the hypodermis.

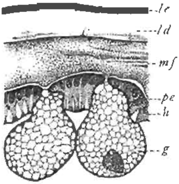

Fig. 113.—Molting-fluid glands of the last larval instar of *Leptinotarsa decimlineata*, just before pupation; *le*, larval epidermis; *ld*, larval dermis; *mf*, molting fluid; *pe*, forming pupal epidermis; *h*, hypodermis; *g*, molting fluid gland (After Tower).

The Molting-fluid glands.—Under this head are classed those unicellular, hypodermal glands that secrete a fluid that facilitates the process of molting, as described in the next chapter (Fig. 113).

While molting-fluid glands are very numerous and conspicuous in certain insects, those living freely exposed where there exists the greatest liability to rapid desiccation, Tower ('06) states that he has never found these glands in larvæ that live in burrows, or in the soil, or in cells; in these cases the molting fluid is apparently secreted by the entire hypodermal layer.

Glands connected with setæ.—There are in insects several kinds of glands in which the outlet of the gland is through the lumen of a seta. The function of the excretions of these glands is various as indicated below. There are also differences in the manner of issuance of the excretion from the seta. In some cases, as in the tenent hairs on the feet of certain insects, the excretion can be seen to issue through a pore at the tip of the seta. In some kinds of venomous setæ the tip of the seta breaks off in the wound made by it and thus sets free the venom. But in most cases the manner of issuance has not been determined, although it is commonly believed to be by means of a minute pore or pores in the seta, the thickness of the wall of the seta making it improbable that the excretion passes from the seta by osmosis.

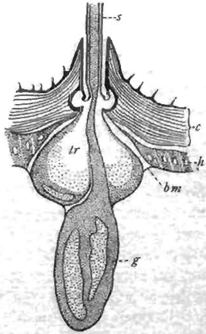

Fig. 114.—Glandular seta; *s*, seta; *c*, cuticula; *h*, hypodermis; *bm*, basement membrane; *tr*, trichogen; *g*, gland (After Holmgren).

The structure of a glandular seta is illustrated by Figure 114; the essential difference between such a seta and an ordinary one, that is a

clothing hair, is that there is connected with it, in addition to the trichogen cell which produced it, the gland cell which opens through it.

In most of the published figures of glandular setæ there is no indication that these organs are supplied with nerves; but in some cases a nerve extending to the gland cell is clearly shown. This condition may be found to be general when more extended investigations of glandular cells have been made. The best known kinds of glandular setæ are the following:

Venomous setæ and spines.—These are best known in larvæ of Lepidoptera, several common species of which possess stinging hairs; among these are *Lagoa crispata*, *Sibine stimulea*, *Automeris io*, and the brown-tail moth, *Euproctis chrysorrhœa*.

Androconia.—The term androcōnia* is applied to some peculiarly modified scales on the wings of certain male butterflies. These are the outlets of glands, which secrete a fluid with an agreeable odor; the supposed function of which is to attract the opposite sex, like the beautiful plumage and songs of male birds. The androconia differ marvelously from ordinary scales in the variety of their forms (Fig. 115). They usually occur in patches on the upper surface of the fore wings; and are usually concealed by other scales; but they are scattered in some butterflies. The most familiar examples of grouped androconia are those that occur in the discal stigma of the hair-streaks, in the brand of certain skippers and in the costal fold of others, and in the scent-pouch of the male of the monarch butterfly.

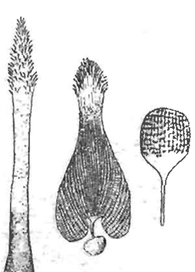

Fig. 115.—Androconia from the wings of male butterflies (After Kellogg).

The specific scent-glands of females.—The well-known fact that if an unfertilized female moth be confined in a cage or otherwise in the open many males of the same species as the female will be attracted to it, and sometimes evidently from a great distance, leads to the conclusion that there must emanate from the female a specific odor. The special glands producing this odor have not been recognized.

Tenent hairs.—In many insects the pulvilli or the empodia are clothed with numerous hairs that are the outlets of glands which

*Androcōnia: andro- (ἀνήρ, ἀνδρός), male; conia (κονία), dust.

secrete an adhesive fluid; this enables the insect to walk on the lower surface of objects (Fig. 116).

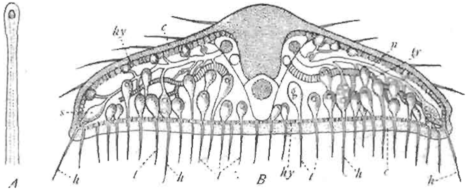

Fig. 116.—A, terminal part of a tenent hair from *Eupolus*, showing canal in the hair and opening near the tip; B, cross-section through a tarsal segment of *Telephorus*; *c*, cuticula; *g*, gland of tenent hair; *h*, *h*, tactile hairs; *hy*, hypodermis; *n*, nerve; *s*, sense-cell of tactile hair; *t*, *t*, tenent hairs (After Dewitz).

The osmeteria.—In many insects there are hypodermal glands that open into sac-like invaginations of the body-wall which can be evaginated when the insect wishes to make use of the secretion produced by these glands; such an organ is termed an *osmeterium*. The invagination of the osmeterium admits of an accumulation of the products of the gland within the cavity of the sac thus formed; when the osmeterium is evaginated the secretion becomes exposed to the air, being then on the outside of the osmeterium, and rapid diffusion of the secretion results.

The most familiar examples of osmeteria are those of the larvæ of the swallow-tailed butterflies, which are forked, and are thrust out from the upper part of the prothorax when the caterpillar is disturbed, and which diffuse a disagreeable odor (Fig. 117). They are obviously organs of defense.

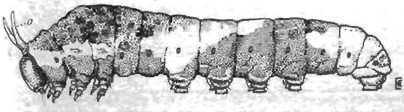

Fig. 117.—Larva of *Papilio thoas*; *o*, osmeterium expanded.

Osmeteria are present in the larvæ of certain blue butterflies, Lycænidæ. These are in the seventh and eighth abdominal segments, and secrete a honey-dew, which attracts ants that attend and probably protect the larvæ. The osmeteria of many other caterpillars have been described.

Glands opening on the surface of the body.—There are several kinds of hypodermal glands, differing widely in function, that open on the surface of the body; among the best known of these are the following:

Wax-glands.—The worker honeybee has four pairs of wax-glands; these are situated on the ventral wall of the second, third, fourth, and fifth abdominal segments, and on that part of the segment which is overlapped by the preceding segment; each gland is simply a disc-like area of the hypodermis (Fig. 118). The cuticle covering each gland is smooth and delicate, and is known as a wax plate. The wax exudes through these plates and accumulates, forming little scales, which are used in making the honey-comb.

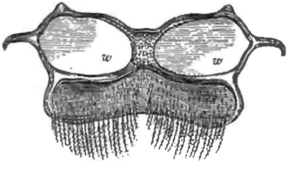

Fig. 118.—Wax-plates of the honeybee (After Cheshire).

Wax-glands exist in many of the Homoptera. In some of these the unicellular wax-glands are distributed nearly all over the body; and the product of these glands forms, in some, a powdery covering; in others, a clothing of threads; and in still others, a series of plates (Fig. 119). Certain coccids excrete wax in considerable quantities. China wax, which was formerly an article of commerce, is the excretion of a coccid known as Pe-la (*Ericerus Pe-la*).

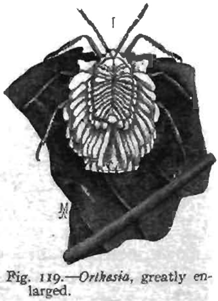

Fig. 119.—*Orthesia*, greatly enlarged.

Froth-glands of spittle-insects.—In the spittle-insects (Cercopidæ) there are large hypodermal glands in the pleural regions of the seventh and eighth abdominal segments, which open through numerous minute pores in the cuticula. These glands secrete a mucilaginous substance, which is mixed with a fluid excreted from the anus, and thus fits it for the retention of bubbles of air included in it by means of abdominal appendages (Guilbeau '08).

Stink-glands.—Glands that secrete a liquid having a fetid odor and that are doubtless defensive exist in many insects. In the stink-bugs

(Pentatomidæ) the fluid is excreted through two openings, one on each side of the lower side of the body near the middle coxæ; in the bed-bug (*Cimex*), the stink-glands open in the dorsal wall of the first three abdominal segments; in *Dytiscus*, the glands open on the prothorax; and in certain Coleoptera they open near the caudal end of the body. These are merely a few examples of the many glands of this type that are known.

The cephalic silk-glands.—In the Lepidoptera, Trichoptera, and Hymenoptera, there is a pair of glands that secrete silk, and which open through the lower lip. These glands are designated as the cephalic silk-glands to distinguish them from the silk-glands of certain Neuroptera and Coleoptera in which the silk is produced by modified Malpighian vessels and is spun from the anus.

The cephalic silk-glands are elongate and coiled; they often extend nearly the whole length of the body; the two ducts unite and the single terminal duct opens through the lower lip, and is not connected with the mouth cavity. These glands are a pair of salivary glands which have been transformed into silk organs. According to Carrière

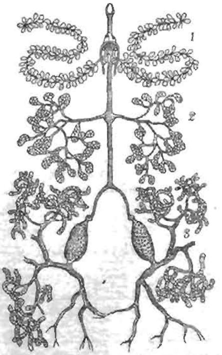

Fig. 120.—The salivary glands of the honeybee (After Cheshire).

Fig. 121.—The mandibular gland of a honeybee.

and Burger ('97), who studied their development in the embryo of a bee, they are developed from the rudiments of the spiracles of the first thoracic segment. In the later development they move

cephalad and the paired openings become a single one. This is the reason that in the adult there are no spiracles in the prothorax.

The Salivary glands.—The term salivary glands is a general one, applied to various glands opening in the vicinity of the mouth. The number of these varies greatly in different insects; the maximum number is found in the Hymenoptera. In the adult worker honey-bee, for example, there are four pairs of glands opening into the mouth; three of these are represented in Figure 120 and the fourth in Figure 121. These are designated as the supracerebral glands (Fig. 120, *1*), the postcerebral glands (Fig. 120, *2*), the thoracic glands (Fig. 120, *3*), and the mandibulary glands (Fig. 121), respectively.

II. THE MUSCLES

There exist in insects a wonderfully large number of muscles; some of these move the segments of the body, others move the appendages of the body, and still others are found in the viscera. Those of the viscera are described later in the accounts of the organs in which they occur.

The muscles that move the segments of the body form several layers just within the body-wall, to which they are attached. The inner layer of these is well shown in Figure 122, which is a copy of one of the plates in the great work by Lyonet (1762) on the anatomy of a caterpillar, *Cossus ligniperda*. The two figures on this plate represent two larvæ which have been split open lengthwise, one on the middle line of the back (Fig. 5), and one on the middle line of the ventral surface (Fig. 4); in each case the alimentary canal has been removed, so that only those organs that are attached quite closely to the body-wall are left. The bands of parallel fibers are the muscles that move the segments. It should be borne in mind, however, that only a single layer of muscles is represented in these figures, the layer that would be seen if a caterpillar were opened in the way indicated. When these muscles are cut away many other muscles are found extending obliquely in various directions between these muscles and the body-wall.

In the head and thorax of adult insects the arrangement of the muscles is even more complicated; for here the muscles that move the appendages add to the complexity of the muscular system.

As a rule, the muscles of insects are composed of many distinc[t] fibers, which are not enclosed in tendinous sheaths as with Verte[brates]

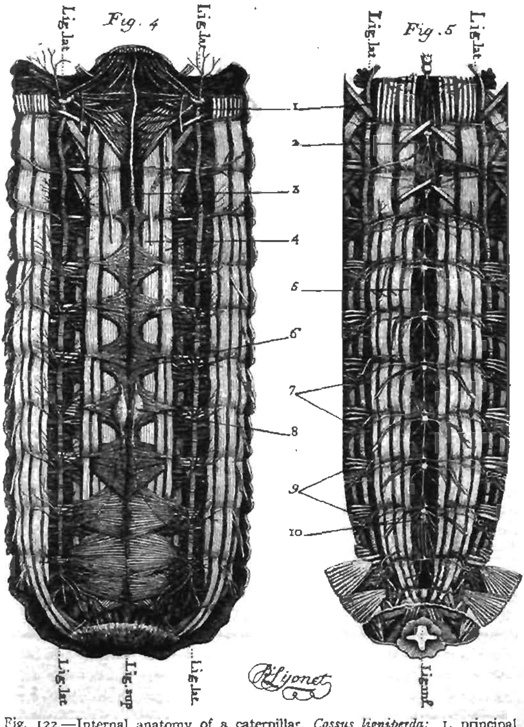

Fig. 122.—Internal anatomy of a caterpillar, *Cossus ligniperda;* 1, principal longitudinal tracheæ; 2, central nervous system; 3, aorta; 4, longitudinal dorsal muscles; 5, longtiudinal ventral muscles; 6, wings of the heart; 7, tracheal trunks arising near the spiracles; 8, reproductive organs; 9, vertical muscles; 10, last abdominal ganglion (From Lyonet).

brates. But the muscles that move the appendages of the body are furnished with a tendon at the end farthest from the body (Fig. 123).

Fig. 123.—A leg of a May-beetle (After Straus-Durckheim).

The muscles of insects appear very differently from those of Vertebrates. *In insects, the* muscles are either colorless and transparent, or yellowish white; and they are soft, almost of a gelatinous consistency notwithstanding this they are very efficient. The fibers of insect muscles are usually, if not always, of the striated type.

Much has been written regarding the muscular power of insects which has been supposed to be extraordinarily great; the power of leaping possessed by many and the great loads, compared to the weight of the body of the insect, that insects have drawn when harnessed to them by experimenters, have been cited as illustrating this. But it has been pointed out that these conclusions are not warranted; that the comparative contractile force of muscles of the same kind depends on the number and thickness of the fibers, that is, on the comparative areas of the cross-sections of the muscles compared; that this sectional area increases as the square of any linear dimension, while the weight of similar bodies increases as the cube of any linear dimension; and consequently, that the muscles of the legs of an insect one fourth inch long and supporting a load 399 times its own weight, would be subjected to the same stress, per square inch of cross-section, as they would be in an insect 100 inches long of precisely similar shape, that carried only its own weight. We thus see that it is the small size of insects rather than an unusual strength of their muscles, that makes possible the apparently marvelous exhibitions of muscular power.

Detailed accounts of the arrangement of the muscles in particular insects have been published by various writers; among the more important of these monographs are the following: Lyonet (1762), on the larva of a cossid moth; Straus-Durckheim (1828), on a May-beetle; Newport (1839), on the larva of a Sphinx moth; Lubbock (1858), on the larva *Pygæra bucephala;* and Berlese ('09a), on several insects.

III. THE ALIMENTARY CANAL AND ITS APPENDAGES

a. THE MORE GENERAL FEATURES

The alimentary canal is a tube extending from one end of the body to the other. In some larvæ, its length is about the same as that of the body; in this case it extends in a nearly straight line, occupying

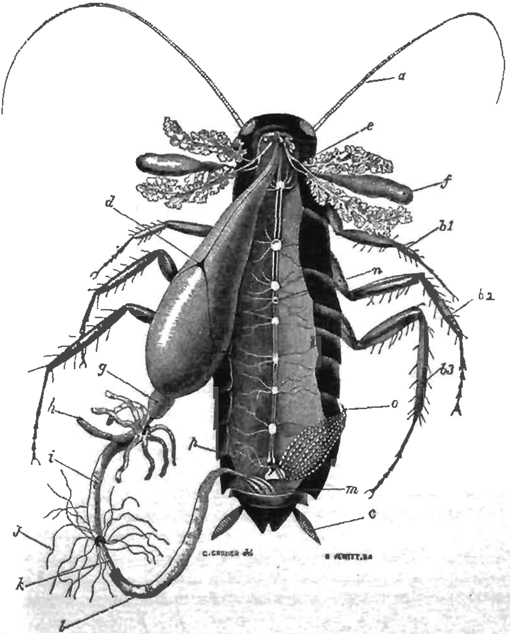

Fig. 124.—Internal anatomy of a cockroach, *Periplaneta orientalis*; *a*, antennæ; b_1, b_2, b_3, first, second, and third legs; *c*, cerci; *d*, ventricular ganglion; *e*, salivary duct; *f*, salivary bladder; *g*, gizzard or proventriculus; h, hepatic cœca; *i*, mid-intestine; *j*, Malpighian vessels; *k*, small intestine; *l*, large intestine; *m*, rectum; *n*, first abdominal ganglion; *o*, ovary; *p*, sebaceous glands (From Rolleston).

the longitudinal axis of the body, as is represented in the diagram given above (Fig. 105). In most insects, however, it is longer than the body, and is consequently more or less convoluted (Fig. 124) great variations exist in the length of the alimentary canal as compared to the length of the body; it is longer in herbivorous insects than it is in those that are carnivorous.

The principal divisions.—Three chief divisions of the alimentary canal are recognized; these are termed the *fore-intestine*, the *mid-intestine*, and the *hind-intestine*, respectively. In the embryological development of the alimentary canal, the fore-intestine and the hind-intestine each arises as an invagination of the ectoderm, the germ layer from which the hypodermis of the body-wall is derived (p. 29). The invagination at the anterior end of the body, which develops into the fore-intestine, is termed the *stomodæum;* that at the posterior end, which develops into the hind-intestine, the *proctodæum.* Between these two deep invaginations of the outer germ layer of the embryo the stomodæum and the proctodæum, and ultimately connecting them, there is developed an entodermal tube, the *mesĕnteron*, which becomes the mid-intestine.

These embryological facts are briefly stated here merely to elucidate two important features of the alimentary canal: first, the fore-intestine and the hind-intestine are invaginations of the body wall and consequently resemble it in structure, the chitinous lining of these two parts of the alimentary canal is directly continuous with the cuticula of the body wall, and the epithelium of these two parts and the hypodermis are also directly continuous; and second, the striking differences, pointed out later, in the structure of the mid-intestine from that of the fore- and hind-intestines are not surprising when the differences in origin are considered.

Imperforate intestines in the larvæ of certain insects.—In the larvæ of certain insects the lumen of the alimentary canal is not a continuous passage; in these larvæ, while food passes freely from the fore-intestine to the mid-intestine, there is no passage of the waste from the mid-intestine to the hind-intestine; there being a construction at the point where the mid-intestine and hind-intestine join, which closes the passage during a part or the whole of the larval life. This condition has been observed in the following families:—

(a) *Hymenoptera.*—Proctotrypidæ (in the first larval instar Ichneumonidæ, Formicidæ, Vespidæ, and Apidæ.

(b) *Diptera.*—Hippoboscidæ.

(*c*) *Neuroptera*.—Myrmeleonidæ, Osmylidæ, Sisyridæ, and Chrysopidæ. In these families the larvæ spin silk from the anus.

(*d*) *Coleoptera*.—In the Campodeiform larvæ of Stylopidæ and Meloidæ.

b. THE FORE-INTESTINE

The layers of the fore-intestine.—The following layers have been recognized in the fore-intestine:

The intima.—This is a chitinous layer which lines the cavity of the fore-intestine; it is directly continuous with the cuticula of the body-wall; and is molted with the cuticula when this is molted.

The epithelium.—This is a cell layer which is continuous with the hypodermis; it is sometimes quite delicate so that it is difficult to demonstrate it.

The basement membrane.—Like the hypodermis the epithelium is bounded on one side by a chitinous layer and on the other by a basement membrane.

The longitudinal muscles.—Next to the basement membrane there is a layer of longitudinal muscles.

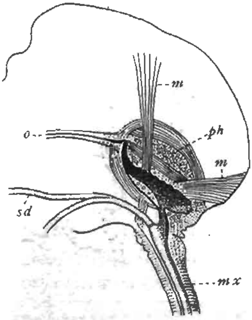

Fig. 125.—Longitudinal section through the head of *Anosa plexippus*, showing the interior of the left half; *mx*, left maxilla, the canal of which leads into the pharynx; *ph*, pharynx; *o*, oesophagus; *m*, *m*, muscles of the pharynx; *sd*, salivary duct (After Burges).

The circular muscles.—Outside of the longitudinal muscles there is a layer of circular muscles.

The peritoneal membrane.—Surrounding the alimentary canal there is a coat of connective tissue, which is termed the peritoneal membrane. This is one of a few places in which connective tissue, so abundant in Vertebrates, is found in insects.

The regions of the fore-intestine.—Several distinct regions of the fore-intestine are recognized; but the extent of these regions differ greatly in different insects.

The pharynx.—The pharynx is not a well-defined region of the intestine; the term pharynx is commonly applied to a region between the mouth and the œsophagus; in mandibulate insects the pharynx

is not distinct from the mouth-cavity; but in sucking insects the pharynx is a highly specialized organ, being greatly enlarged, muscular, and attached to the wall of the head by muscles. It is the pumping organ by which the liquid food is drawn into the alimentary canal. The pharnyx of the milkweed butterfly (Fig. 125) is a good example of this type of pharynx.

The œsophagus.—The œsophagus is a simple tube which traverses the caudal part of the head and the cephalic part of the thorax. There are variations in the application of the term œsophagus depending on the presence or absence of a crop and of a proventriculus, which are modified portions of the œsophagus; when either or both of these are present, the term œsophagus is commonly restricted to the unmodified part of the fore-intestine.

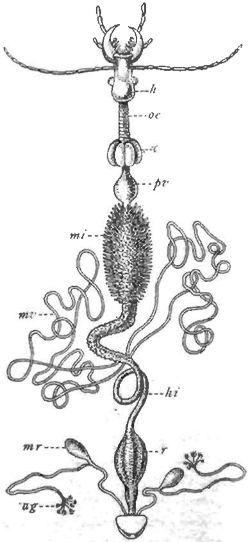

Fig. 126.—Alimentary canal of *Carabu auratus; h*, head; *oe*, œsophagus; *c* crop; *pv*, proventriculus; *mi*, mid intestine covered with villiform gastri cœca; *mv*, Malpighian vessels; *hi*, par of hind-intestine; *r*, rectum; *ag*, ana glands: *mr*, muscular reservoir (After Dufour).

The crop.—In many insects a portion of the œsophagus is dilated and serves as a reservoir of food; this expanded part, when present, is termed the *crop*. In the cockroach (Fig. 124) it is very large, comprising the greater part of the fore-intestine; in the ground-beetle *Carabus* (Fig. 126, *c*), it is much more restricted; this is the case also in the honeybee, where it is a nearly spherical sac in which the nectar is stored as it is collected from flowers and carried to the hive. In some insects the crop is a lateral dilatation of the œsophagus, and in some of these it is stalked.

The proventriculus.—In certain insects that feed on hard substances, the terminal portion of the fore-intestine, that part im-

mediately in front of the mid-intestine or ventriculus, is a highly specialized organ in which the food is prepared for entrance into the more delicate ventriculus; such an organ is termed the *proventriculus* (Fig. 126, *pv*). The characteristic features of a proventriculus are a remarkable development of the chitinous intima into folds and teeth and a great increase in the size of the muscles of this region. The details of the structure of this organ vary greatly in different insects; a cross-section of the proventriculus of the larva of *Corydalus* (Fig. 127) will serve to illustrate its form. In the proventriculus, the food is both masticated and more thoroughly mixed with the digestive fluids.

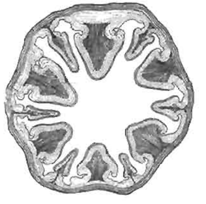

Fig. 127.—Cross-section of the proventriculus of a larva of *Corydalus*.

The œsophageal valve.—When the fore-intestine projects into the mid-intestine, as shown in Figure 128, the folded end of the fore-intestine is termed the *œsophageal valve*.

c. THE MID-INTESTINE

The mid-intestine is the intermediate of the three principal divisions of the alimentary canal, which are distinguished by differences in their embryological origins, as stated above. The mid-intestine is termed by different writers the *mesĕnteron*, the *stomach*, the *chylific ventricle*, the *chylestomach*, and the *ventrĭculus*.

The layers of the mid-intestine.—The structure of the mid-intestine differs markedly from that of the fore-intestine. In the mid-intestine there is no chitinous intima, and the relative positions of the circular and longitudinal muscles are reversed.

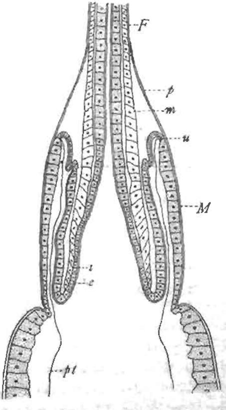

Fig. 128.—The œsophageal valve of a larva of *Simulium*; F, fore-intestine: M, mid-intestine; *u*, point of union of fore-intestine and mid-intestine; *p*, peritoneal membrane; *i*, intima of fore-intestine; *e*, epithelium of fore-intestine; *pl*, peritrophic membrane; *m*, muscles

The sequence of the different layers is as follows: a lining *epithelium*, which is supported by a *basement membrane*, a layer of *circular muscles*, a layer of *longitudinal muscles*, and a *peritoneal membrane*.

The epithēlium.—The epithelium of the mid-intestine is very conspicuous, being composed of large cells, which secrete a digestive fluid. These cells break when they discharge their secretion and are replaced by new cells, which are developed in centers termed *nidi* (Fig. 129, *n*).

The extent of the digestive epithelium is increased in many insects by the development of pouch-like diverticula of the mid-intestine, these are the *gastric cœca* (Fig. 124, *h*). These differ greatly in number in different insects and are wanting in some. In some predaceous beetles they are villiform and very numerous (Fig. 126, *mi*).

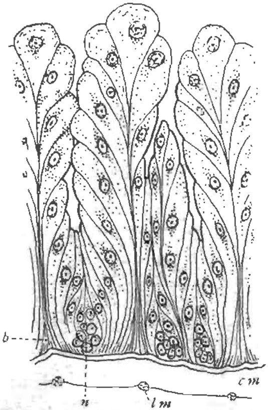

Fig. 129.—Resting epithelium of mid-intestine of a dragon-fly naiad *b*, bases of large cells filled with digestive fluid; *cm*, space filled by circular muscles; *lm*, longitudinal muscles; *n*, nidus in which new cells are developing (From Needham).

The peritrophic membrane.—In many insects there is a membranous tube which is formed at or near the point of union of the fore-intestine and the mid-intestine and which incloses the food so that it does not come in contact with the delicate epithelium of the mid-intestine; this is known as the *peritrophic membrane* (Fig. 128, *pt*). As a rule this membrane is found in insects that eat solid food and is lacking in those that eat liquid food. It is obvious that the digestive fluid and the products of digestion pass through this membrane. It is continuously formed at its point of origin and passes from the body inclosing the excrement.

d. THE HIND-INTESTINE

The layers of the hind-intestine.—The layers of the hind-intestine are the same as those of the fore-intestine described above, except that a greater or less number of circular muscles exist between the basement membrane of the epithelial layer and the layer of longitudinal muscles. The

sequence of the layers of the hind-intestine is, therefore, as follows: the *intima*, the *epithelium*, the *basement membrane*, the *ental circular muscles*, the *longitudinal muscles*, the *ectal circular muscles*, and the *peritoneal membrane*.

The regions of the hind-intestine.—Three distinct regions are commonly recognized in the hind-intestine, these are the *small intestine* (Fig. 124, *k*), the *large intestine* (Fig. 124, *l*), and the *rectum* (Fig. 124, *m*).

The Malpighian vessels.—There open into the beginning of the hind-intestine two or more simple or branched tubes (Fig. 124, *j*), these are the *Malpighian vessels*. The number of these vessels varies in different insects but is very constant within groups; there are either two, four, or six of them; but, as a result of branching, there may appear to be one hundred or more. The function of the Malpighian vessels has been much discussed; it was formerly believed to be hepatic, but now it is known that normally it is urinary.

The Malpighian vessels as silk-glands.—There are certain larvæ that in making their cocoons spin the silk used from the anus. These larvæ are chiefly found among those in which the passage from the mid-intestine to the hind-intestine is closed. The silk spun from the anus is secreted by the Malpighian vessels.

Among the larvæ in which the Malpighian vessels are known to secrete silk are those of the Myrmeleonidæ, *Osmylus* (Hagen 1852), *Sisyra* (Anthony '02), *Lebia scapularis* (Silvestri '05), and the Coccidæ (Berlese '96). Berlese states that the Malpighian vessels secrete the woof of the scale of the Coccidæ.

The cæcum.—In some insects there is a pouch-like diverticulum of the rectum, this is the *cæcum*.

The anus.—The posterior opening of the alimentary canal, the *anus*, is situated at the caudal end of the abdomen.

IV. THE RESPIRATORY SYSTEM

Insects breathe by means of a system of air-tubes, which ramify in all parts of the body and its appendages; these air-tubes are of two kinds, which are termed *tracheæ* and *tracheoles*, respectively. In adult insects and in most nymphs and larvæ, the air is received through openings in the sides of the segments of the body, which are known as *spĭracles* or *stigmăta*.

Many insects that live in water are furnished with special devices for obtaining air from above the water; but with naiads and a few

aquatic larvæ the spiracles are closed; in these insects the air is purified by means of gill-like organs, termed *tracheal gills*. A few insects have *blood-gills*.

Two types of respiratory systems, therefore, can be recognized: first, the *open type*, in which the air is received through spiracles; and second, the *closed type*, in which the spiracles are not functional.

a. THE OPEN OR HOLOPNEUSTIC TYPE OF RESPIRATORY ORGANS

That form of respiratory organs in which the tracheæ communicate freely with the air outside the body through open spiracles is termed the open or holopneustic type.*

As the open type of respiratory organs is the most common one, those features that are common to both types will be discussed under this head as well as those that are peculiar to this type. Under the head of closed respiratory organs will be discussed only those features distinctly characteristic of that type.

1. The Spiracles

The position of the spiracles.—The spiracles are situated one on each side of the segments that bear them or are situated on the lateral aspects of the body in the transverse conjunctivæ.

The question of the position of the spiracles has not been thoroughly investigated; but I believe that normally the tracheæ, of

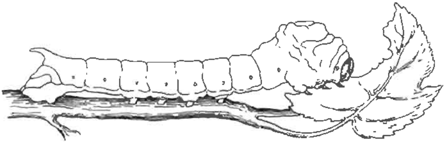

Fig. 130.—Lateral view of a silkworm showing the spiracles (After Verson)

which the spiracles are the mouths, are invaginations of the transverse conjunctivæ between segments. From this normal position a spiracle may migrate either forward or backward upon an adjacent segment (Fig. 130).

The number of spiracles.—The normal number of spiracles is ten pairs; when in their normal position, there is a pair in front of the

*Hŏlopneustic: *holo* (ὅλος), *whole; pneuma* (πνεῦμα), *breath*.

second and third thoracic segments and the first to the eighth abdominal segments, respectively. There are none in the corresponding position in front of the first thoracic segment. See account of cephalic silk-glands p. 103.

The two pairs of thoracic spiracles are commonly distinguished as the mesothoracic and the metathoracic spiracles; that is each pair of spiracles is attributed to the segment in front of which it is normally situated. Following this terminology there are no prothoracic spiracles; although sometimes the first pair of spiracles is situated in the hind margin of the prothorax, having migrated forward from its normal position. It would be better to designate the thoracic spiracles as the first and second pairs of thoracic spiracles, respectively; in this way the same term would be applied to a pair of spiracles whatever its position. There are many references in entomological works to "prothoracic spiracles," but these refer to the pair of spiracles that are more commonly designated the mesothoracic spiracles.

In many cases the abdominal spiracles have migrated back upon the segment in front of which they are normally situated, being frequently situated upon the middle of the segment.

The statements made above refer to the normal number and distribution of spiracles; but a very wide range of variations from this type exists. Perhaps the most abnormal condition is that found in the genus *Smynthurus* of the Collembola, where there is a single pair of spiracles which is borne by the neck. In the Poduridæ, also of the Collembola, the respiratory system has been lost, there being neither tracheæ nor spiracles.

Terms indicating the distribution of the spiracles.—The following terms are used for indicating the distribution of the spiracles; they have been used most frequently in descriptions of larvæ of Diptera. These terms were formed by combining with *pneustic* (from *pneo*, to breathe) the following prefixes: *peri-*, around, about; *pro-*, before; *meta-* after; and *amphi*, both.

Peripneustic.—Having spiracles in a row on each side of the body, the normal type.

Propneustic.—With only the first pair of spiracles.

Metapneustic.—With only the last pair of spiracles.

Amphipneustic.—With a pair of spiracles at each end of the body.

The structure of spiracles.—In their simplest form the spiracles or stigmata are small round or oval openings in the body-wall. In many cases they are provided with hairs to exclude dust; in some, as in the larva of *Corydalus*, each spiracle is furnished with a lid (Fig. 131, *a*); in fact, very many forms of spiracles exist. Usually each spiracle opens by a single aperture; but in some larvæ and pupæ of Diptera they have several openings (Fig. 131, *b*).

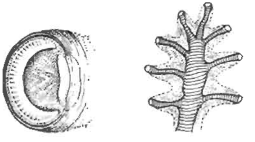

Fig. 131.—Spiracles; *a*, of the larva of *Corydalus*; *b*, of the larva of *Drosophila amœna*.

The closing apparatus of the tracheæ.—Within the body, a short distance back of the spiracle, there is an apparatus consisting of several chitinous parts, surrounding the trachea, and moved by a muscle, by which the trachea can be closed by compression (Fig. 132). This is the *closing apparatus of the trachea*. The closing of this apparatus and the contraction of the body by the respiratory muscles is supposed to force the air into the tracheoles, which are the essential respiratory organs.

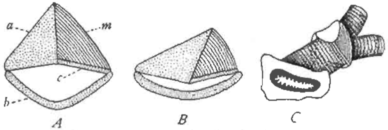

Fig. 132.—Diagrams representing the closing apparatus of the tracheæ; *a*, *b*, *c*, chitinous parts of the apparatus; *m*, muscle; A, apparatus open; B, apparatus closed; C, spiracle and trunk of trachea showing the position of the apparatus. (From Judeich and Nitsche).

2. THE TRACHEÆ

Each spiracle is the opening of an air-tube or trachea. The main tracheal trunk which arises from the spiracle soon divides into several branches, these in turn divide, and by repeated divisions an immense number of branches are formed. Every part of the body is supplied with tracheæ.

In a few insects the group of tracheæ arising from a spiracle is not connected with the groups arising from other spiracles; this is the case in *Machilis* (Fig. 133). In most insects, however, each group of tracheæ is connected with the corresponding groups in adjacent seg-

ments by one or more longitudinal tracheæ, and is also connected

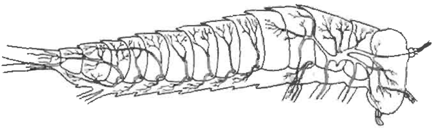

Fig. 133.—The tracheæ of *Machilis* (From Oudemans).

with the group on the opposite side of the same segment by one or more transverse tracheæ (Fig. 134)

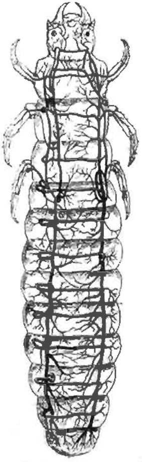

Fig. 134.—Larva of *Cantharis vesicatoria*, showing the distribution of tracheæ (From Henneguy after Beauregard).

The structure of the tracheæ.—The fact that in their embryological development the tracheæ arise as invaginations of the body-wall, makes it easy to understand the structure of the tracheæ. The three layers of the body-wall are directly continuous with corresponding layers in the wall of a trachea (Fig. 135). These layers of a trachea are designated as the *intima*, the *epithelium*, and the *basement membrane*.

The *intima* is the chitinous inner layer of the tracheæ. It is directly continuous with the cuticula of the body-wall, and like the cuticula is molted at each ecdysis.

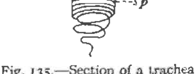

Fig. 135.—Section of a trachea and the body-wall: *c*, cuticula; *h*, hypodermis; *bm*, basement membrane; *sp*, spiral thickening of the intima, the tænidium.

A peculiar feature of the intima of tracheæ is the fact that it is furnished with thickenings which extend spirally. These give the tracheæ their characteristic transversely striated appearance. If a piece of one of the larger tracheæ be pulled apart the intima will tear between the folds of the spiral thickening, and the latter will uncoil from within the trachea like a

thread (Fig. 135). The spiral thickening of the intima of a trachea is termed the *tænidium*. In some insects there are several parallel tænidia; so that when an attempt is made to uncoil the thread a ribbon-like band is produced, composed of several parallel threads. This condition exists in the larger tracheæ of the larva *Corydalus*.

The *epithēlium* of the trachea is a cellular layer, which is directly continuous with the hypodermis of the body-wall.

The *basement membrane* is a delicate layer, which supports the epithelium, as the basement membrane of the body-wall supports the hypodermis.

3. *The Tracheoles*

The tracheoles are minute tubes that are connected with the tips of tracheæ or arise from their sides, but which differ from tracheæ in their appearance, structure, and mode of origin; they are not small tracheæ, but structures that differ both histologically and in their origin from tracheæ.

The tracheoles are exceedingly slender, measuring less than one micron in diameter; ordinarily they do not taper as do tracheæ; they contain no tænidia; and they rarely branch, but often anastomose, which gives them a branched appearance (Fig. 136, *t* and 138 B, *t*).

Each tracheole is of unicellular origin, and is, at first, intracellular in position, being developed coiled within a single cell of the epithelium of a trachea. In this stage of its development it has no connection with the lumen of the trachea in the wall of which it is developing, being separated from it by the intima of the trachea. A subsequent molting of the intima of the trachea opens a connection between the lumen of the tracheole and the trachea. At the same time or a little later the tracheole breaks forth from its mother cell, uncoils, and extends far beyond the cell in which it was developed.

The tracheoles are probably the essential organs of respiration, the tracheæ acting merely as conduits of air to the tracheoles.

4. *The Air-Sacs*

In many winged insects there are expansions of the tracheæ, which are termed *air-sacs*. These vary greatly in number and size. In the honeybee there are two large air-sacs which occupy a considerable part of the abdominal cavity; while in a May-beetle there are hundreds of small air-sacs. The air-sacs differ from tracheæ in lacking tænidia.

As the air-sacs lessen the specific gravity of the insect they probably aid in flight; as filling the lungs with air makes it easier for a man to float in water; in each case there is a greater volume for the same weight.

5. Modifications of the open type of respiratory organs in aquatic insects

There are many insects in which the spiracles are open that live in water; these insects breathe air obtained from above the surface of the water. Some of these insects breathe at the surface of the water,

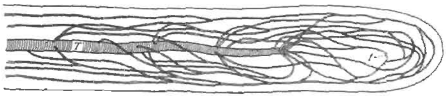

Fig. 136.—Part of a tracheal gill of the larva of *Corydalus;* T, trachea; *t*, tracheoles.

as the larvæ and pupæ of mosquitoes, the larvæ of *Eristalis*, and the Nepidæ; others get a supply of air and carry it about with them beneath the surface of the water, as the Dytiscidæ, the Notonectidæ and the Corisidæ. The methods of respiration of these and of other aquatic insects with open spiracles are described in the accounts of these insects given later.

b. THE CLOSED OR APNEUSTIC TYPE OF RESPIRATORY ORGANS

That type of respiratory organs in which the spiracles do not function is termed the closed or apneustic* type; it exists in naiads and in a few aquatic larvæ.

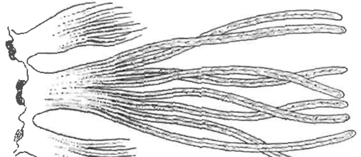

Fig. 137.—Part of a tuft of tracheal gills of a larva of *Corydalus*.

1. The Tracheal Gills

In the immature insects mentioned above, the air in the body is purified by means of organs known as *tracheal gills*.

*Apneustic: *apneustos* (ἄπνευστος), without breath.

These are hair-like or more or less plate-like expansions of the body-wall, abundantly supplied with tracheæ and tracheoles. Figures 136 and 137 represents a part of a tuft of hair-like tracheal gills of a larva of *Corydalus* and figure 138 a plate-like tracheal gill of a naiad of a damsel-fly. In these tracheal gills the tracheoles are separated from the air in the water only by the delicate wall of the tracheal gill which admits of the transfer of gases between the air in the tracheoles and the air in the water.

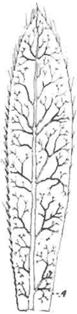

Fig. 138.—Tracheal gill of a damsel-fly: A, entire gill showing the tracheæ; B, part of gill more magnified showing both tracheæ (T) and tracheoles (t).

Tracheal gills are usually borne by the abdomen, sometimes by the thorax, and in case of one genus of stone-flies by the head. They pertain almost exclusively to the immature stages of insects; but stone-flies of the genus *Pteronarcys* retain them throughout their existence. In the naiads of the Odonata the rectum is supplied with many tracheæ and functions as a tracheal gill.

2. Respiration of Parasites

It is believed that internal parasitic larvæ derive their air from air that is contained in the blood of their hosts, and that this is done by osmosis through the cuticula of the larva, the skin of the larva being furnished with a network of fine tracheæ (Seurat '99).

3. The blood-gills

Certain aquatic larvæ possess thin transparent extensions of the body wall, which are filled with blood, and serve as respiratory organs. These are termed *blood-gills*.

Blood-gills have been observed in comparatively few insects; among them are certain trichopterous larvæ; the larva of an exotic beetle, *Pelobius;* and a few aquatic dipterous larvæ, *Chironomus* and *Simulium*. It is probable that the ventra sacs of the Thysanura, described in the account of that order, are also blood-gills.

V. THE CIRCULATORY SYSTEM

The general features of the circulatory system.—In insects the circulatory system is not a closed one, the blood flowing in vessels during only a part of its course. The greater part of the circulation of this fluid takes place in the cavities of the body and of its appendages, where it fills the space not occupied by the internal organs.

Almost the only blood-vessel that exists in insects lies just beneath the body-wall, above the alimentary canal (Fig. 105, *h*). It extends from near the caudal end of the abdomen through the thorax into the head. That part of it that lies in the abdomen is the *heart;* the more slender portion, which traverses the thorax and extends into the head is the *aorta*.

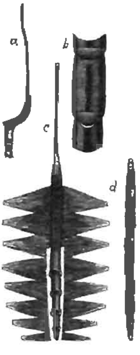

Fig. 139.—Heart of a May-beetle; *a*, lateral aspect of the aorta; *b*, interior of the heart showing valves; *c*, ventral aspect of the heart and wing-muscles, the muscles are represented as cut away from the caudal part of the heart; *d*, dorsal aspect of the heart (After Straus-Durckheim).

On each side of the heart, there is a series of triangular muscles extending from the heart to the lateral wall of the body. These constitute the *dorsal diaphragm* or the *wings of the heart.* They are discussed later under the head: Suspensoria of the Viscera.

The heart.—The heart is a tube, which is usually closed at its posterior end; at its anterior end it is continuous with the aorta. The heart is divided by constrictions into chambers which are separated by valves (Fig. 139). The number of these chambers varies greatly in different insects; in some, as in *Phasma* and in the larva of *Corethra*, there is only one, in others, as in the cockroach, there are as many as thirteen, but usually there are not more than eight. The blood is admitted to the heart through slit-like openings, the *ostia of the heart;* usually there is a pair of ostia in the lateral walls of each chamber. Each ostium is furnished with a valve which closes it when the chamber contracts.

The wall of the heart is composed of two distinct layers: an inner muscular layer; and an outer, connective tissue or peritoneal layer. The muscular layer consists chiefly of annular muscles; but longitudinal fibers have also been observed.

The pulsations of the heart.—When a heart consists of several chambers, they contract one after another, the wave of contraction passing from the caudal end of the heart forwards. As the valves between the chambers permit the blood to move forward but not in the opposite direction, the successive contraction of the chambers causes the blood received through the ostia to flow toward the head, into the aorta.

The aorta.—The cephalic prolongation of the heart, the *aorta* (Fig. 139, *a*), is a simple tube, which extends through the thorax into the head, where it opens in the vicinity of the brain. In some cases, at least, there are valves in the aorta.

The circulation of the blood.—The circulation of the blood can be observed in certain transparent insects, as in young naiads, in larvæ of Trichoptera, and in insects that have just molted. The blood flows from the open, cephalic end of the aorta and passes in quite definite streams to the various parts of the body-cavity and into the cavities of the appendages. These streams, like the ocean currents, have no walls but flow in the spaces between the internal organs. After bathing these organs, the blood returns to the sides of the heart, which it enters through the ostia.

Accessory circulatory organs.—Accessory pulsating circulatory organs have been described in several insects. These are sac-like structures which contract independently of the contractions of the heart. They have been found in the head in several Orthoptera; in the legs of Hemiptera, and in the caudal filaments of Ephemerida.

VI. THE BLOOD

The blood of insects is a fluid, which fills the perivisceral cavity, bathing all of the internal organs of the body, and flowing out into the cavities of the appendages of the body. In only a comparatively small portion of its course, is the blood enclosed in definite blood-vessels; these, the heart and the aorta are described above. The blood consists of two elements, a fluid *plasma* and cells similar to the white corpuscles of the blood of vertebrates, the *leucocytes.*

The blood of insects differs greatly in appearance from the blood of vertebrates, on account of the absence of red blood-corpuscles. In most insects the blood is colorless; but in many species it has a yellowish, greenish, or reddish color. In the latter case, however, the color is not due to corpuscles of the type which gives the characteristic color to the blood of vertebrates.

The leucocytes are nucleated, colorless, amœboid cells similar to the white corpuscles of vertebrates, in appearance and function; they take up and destroy foreign bodies and feed upon disintegrating tissue. It is believed that the products of digestion of disintegrating tissue by the leucocytes pass into the blood and serve to nourish new tissue.

The blood receives the products of digestion of food, which pass in a liquid form, by osmosis, through the walls of the alimentary canal. On the other hand it gives up to the tissues which it bathes the materials needed for their growth. In insects oxygen is supplied to the tissues and gaseous wastes are removed chiefly by the respiratory system and not by means of the blood as in vertebrates.

VII. THE ADIPOSE TISSUE

On opening the body of an insect, especially of a larva, one of the most conspicuous things to be seen is fatty tissue, in large masses. These often completely surround the alimentary canal, and are held in place by numerous branches of the tracheæ with which they are supplied. Other and smaller masses of this tissue adhere to the inner surface of the abdominal wall, in the vicinity of the nervous system, and at the sides of the body. In adult insects it usually exists in much less quantity than in larvæ.

The chief function of the adipose tissue is the storage of nutriment; but it is believed that it also has a urinary function, as concretions of uric acid accumulate in it during the life of the insect.

VIII. THE NERVOUS SYSTEM

a. THE CENTRAL NERVOUS SYSTEM

The more obvious parts of the central nervous system are the following: a ganglion in the head above the œsophagus, the *brain;* a ganglion in the head below the œsophagus, the *subœsophageal ganglion;* a series of ganglia, lying on the floor of the body cavity in the thorax and in the abdomen, the *thoracic* and the *abdominal ganglia;* two longitudinal cords, the *connectives*, uniting all of these ganglia in a series; and many *nerves* radiating from the ganglia to the various parts of the body.

The connectives between the brain and the subœsophageal ganglion pass one on each side of the œsophagus; these are termed the *crura cerebri*, or the legs of the brain; in the remainder of their course, the two connectives are quite closely parallel (Fig. 124).

The series of ganglia is really a double one, there being typically a pair of ganglia in each segment of the body; but each pair of ganglia are more or less closely united on the middle line of the body, and often appear to be a single ganglion.

In some cases the ganglia of adjacent segments coalesce, thus reducing the number of distinct ganglia in the series. It has been demonstrated that the brain is composed of the coalesced ganglia of three of the head segments, and the subœsophageal ganglion of the coalesced ganglia of the remaining four segments.

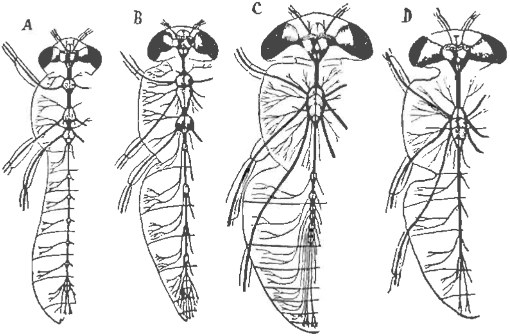

Fig. 140.—Successive stages in the coalescence of thoracic and of abdominal ganglia in Diptera; A, *Chironomus;* B, *Empis;* C, *Tabanus;* D, *Sarcophaga* (From Henneguy after Brandt).

The three parts of the brain, each of which is composed of the pair of ganglia of a head segment, are designated as the ***protocerebrum***, the ***deutocerebrum***, and the ***tritocerebrum***, respectively. The protocerebrum innervates the compound eyes; the deutocerebrum, the antennæ; and the tritocerebrum, the labrum.

The subœsophageal ganglion is composed of four pairs of primary ganglia; these are the ganglia of the segments of which the mandibles, the maxillulæ, the maxillæ, and the labium, respectively, are the appendages.

The three pairs of thoracic ganglia often coalesce so as to form a single ganglionic mass; and usually in adult insects the number of abdominal ganglia is reduced in a similar way.

Successive stages in the coalescence of the thoracic and abdominal ganglia can be seen by a study of the nervous system of the larva, pupa, and adult of the same species, a distinct cephalization of the central nervous system taking place during the development of the insect. Varying degrees of coalescence of the thoracic and of the abdominal ganglia can be seen by a comparative study of the nervous systems of different adult insects (Fig. 140).

The transverse band of fibers that unite the two members of a pair of ganglia is termed a *commissure*. In addition to the commissures that pass directly from one member of a pair of ganglia to the other, there is in the head a commissure that encircles the œsophagus in its passage from one side of the brain to the other, this is the *subœsophageal commissure* (Fig. 141).

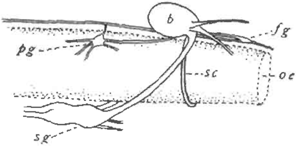

Fig. 141.—Lateral view of the œsophagus of a caterpillar, showing the subœsophageal commissure; *b*, brain; *oe*, œsophagus; *sc*, subœsophageal commissure; *sg*, subœsophageal ganglion; *pg*, paired ganglion (After Liénard).

The nerves that extend from the central chain of ganglia to the different parts of the body are a part of the central nervous system; the core of each nerve fiber being merely a process of a ganglionic cell, however long it may be.

b. THE ŒSOPHAGEAL SYMPATHETIC NERVOUS SYSTEM

In addition to the central nervous system as defined above there are three other nervous complexes which are commonly described as separate systems although they are connected to the central nervous system by nerves. These are the œsophageal sympathetic nervous system, the ventral sympathetic nervous

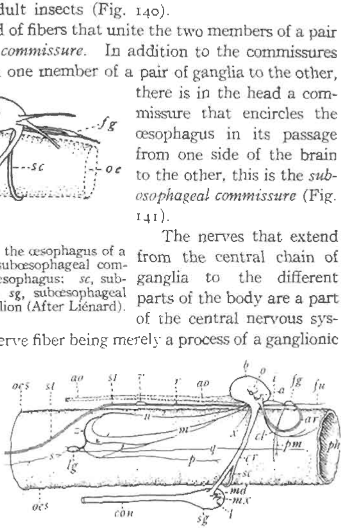

Fig. 142.—Lateral view of the nerves of the head in the larva of *Corydalus; a*, antennal nerve; *ao*, aorta; *ar* paired nerves connecting the frontal ganglion with the brain; *b*, brain; *cl*, clypeo-labral nerve; *con*, connective; *cr*, crura cerebri; *fg*, frontal ganglion; *fn*, frontal nerve; *i*, unpaired nerve connecting the frontal ganglion with the brain; *l*, labial nerve; *lg*, the paired ganglia; *md*, mandibular nerve; *m*, *p*, *q*, *s*, *u*, *z*, nerves of the œsophageal sympathetic system; *mx*, maxillary nerve; *o*, optic nerves; *oes*, œsophagus; *ph*, pharynx; *pn*, pharyngeal nerve; *r*, recurrent nerve; *sc*, subœsophageal commissure; *sg*, subœsophageal ganglion; *st*, stomagastric nerve; *v*, ventricular ganglion (From Hammar).

system, and the peripheral sensory nervous system. The first of these is connected with the brain; the other two, with the thoracic and abdominal ganglia of the central nervous system.

The œsophageal sympathetic nervous system is intimately associated with the œsophagus and, as just stated, is connected with the brain. It is described by different writers under various names; among these are *visceral*, *vagus*, and *stomatogastric*. It consists of two, more or less distinct, divisions, an unpaired median division and a paired lateral division.

The unpaired division of the œsophageal sympathetic nervous system is composed of the following parts, which are represented in Figures 141, 142, 143, and 144: the *frontal ganglion* (*fg*), this is a minute ganglion situated above the œsophagus a short distance in front of the brain; the *unpaired nerve connecting the frontal ganglion with the brain* (*i*), this is a small nerve extending from the brain to the frontal ganglion; the *paired nerves connecting the frontal ganglion with the brain* (*ar*), these are arching nerves, one on each side, extending from the upper ends of the crura cerebri to the frontal ganglion; the *frontal nerve* (*fn*), this nerve arises from the anterior border of the frontal ganglion and extends cephalad into the clypeus, where it bifurcates; the *pharyngeal nerves* (*pn*), these extend, one on each side, from the frontal ganglion to the lower portions of the pharynx; the *recurrent nerve* (*r*), this is a single median nerve, which arises from the caudal border of the frontal ganglion, and extends back, passing under the brain and between the

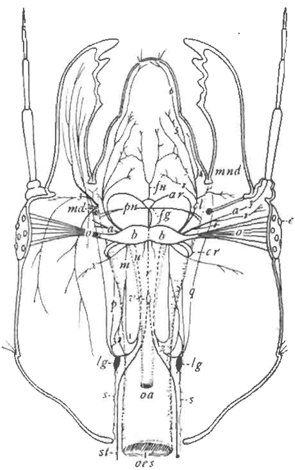

Fig. 143.—Dorsal view of the nerves of the head in the larva of *Corydalus*; *e*, ocelli; *mnd*. mandible; other lettering as in Figure 142 (From Hammar).

aorta and the œsophagus, to terminate in the ventricular ganglion; the *ventricular ganglion* (*v*), this is a minute ganglion on the middle line, a short distance caudal of the brain, and between the aorta and the œsophagus; and the *stomogastric nerves* (*st*), these are two nerves which extend back from the caudal border of the ventricular ganglion, they are parallel for a short distance, then they separate and pass, one on each side, to the sides of the alimentary canal which they follow to the proventriculus.

The paired division of the œsophageal sympathetic nervous system varies greatly in form in different insects. In the larva of *Corydalus*, there is a single pair of ganglia (Fig. 142 and 143, *lg*), one on each side of the œsophagus; each of these ganglia is connected with the brain by two nerves (*m* and *u*) but they are not connected with each other nor with the unpaired division of this system. In a cockroach (Fig. 144), there are two pairs of ganglia (*ag* and *pg*); the two ganglia of each side are connected with each other and with the recurrent nerve of the unpaired division.

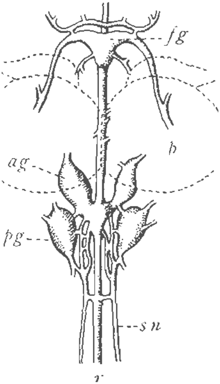

Fig. 144.—The œsophageal sympathetic nervous system of *Periplaneta orientalis;* the outlines of the brain (*b*) and the roots of the antennal nerve which cover a portion of the sympathetic nervous system are given in dotted lines; *ag*, anterior ganglion; *pg*, posterior ganglion; *fg*, frontal ganglion; *sn*, nerves of the salivary glands; *r*, recurrent nerve (After Hofer).

As yet comparatively little is known regarding the function of the œsophageal sympathetic nervous system of insects; nerves extending from it have been traced to the clypeus, the muscles of the pharynx, the œsophagus, the mid-intestine, the salivary glands, the aorta, and the heart. Its function is probably analogous to that of the sympathetic nervous system of Vertebrates.

c. THE VENTRAL SYMPATHETIC NERVOUS SYSTEM

The ventral sympathetic nervous system consists of a series of more or less similar elements, each connected with a ganglion of the ventral chain of the central nervous system. Typically there is an element of this system arising in each thoracic and

abdominal ganglion; and each element consists of a median nerve extending from the ganglion of its origin caudad between the two connectives, a pair of lateral branches of this median nerve, and one or more ganglionic enlargements of each lateral branch. Frequently the median nerve extends to the ganglion of the following segment. A simple form of this system exists in the larva of *Cossus ligniperda* (Fig. 122); and a more complicated one, in *Locusta viridissima* (Fig. 145).

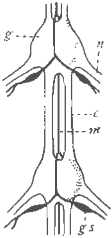

Fig. 145.—Part of the ventral chain of ganglia of *Locusta viridissima* and of the ventral sympathetic nervous system: *g*, ganglion of the central nervous system; *n*, nerve; *c*, connective; *m*, median nerve of the sympathetic system; *gs*, ganglion of the sympathetic system (From Berlese).

From each lateral branch of the median nerve a slender twig extends to the closing apparatus of the tracheæ.

d. THE PERIPHERAL SENSORY NERVOUS SYSTEM

Immediately beneath the hypodermal layer of the body-wall, there are many bipolar and multipolar nerve-cells whose prolongations form a network of nerves; these constitute the *peripheral sensory nervous system* or the *subhypodermal nerve-plexus*.

The fine nerves of this system are branches of larger nerves which arise in the central nervous system; and the terminal prolongations of the bipolar nerve-cells innervate the sense-hairs of the body-wall.

Figure 146 represents a surface view of a small part of the peripheral sensory nervous system of the silkworm, *Bombyx mori*, as figured by Hilton ('02); the bases of several sense hairs are also shown. The details of this figure are as follows: *h*, *h*, *h*, the bases of sense-hairs; *s*, *s*, *s*, bipolar nerve-cells; *m*, *m*, *m* multipolar cells; *n*, *n*, *n*, nerves. All of these structures are united, forming a network. Of especial interest is the fact that the terminal prolongation of each bipolar nerve-cell enters the cavity of a sense-hair and that the other prolongation is a branch of a larger nerve which comes from the central nervous system.

The peripheral sensory nervous system is so delicate that it can not be seen except when it is stained by some dye that differentiates nervous matter from other tissues. For this purpose the intra vitam methylen blue method of staining is commonly used.

IX. GENERALIZATIONS REGARDING THE SENSE-ORGANS OF INSECTS

The sense-organs of insects present a great variety of forms, some of which are still incompletely understood, in spite of the fact that they have been investigated by many careful observers. In the limited space that can be devoted to these organs here only the more general features of them can be described and some of the disputed questions regarding them briefly indicated.

A classification of the sense-organs.—The different kinds of sense-organs are distinguished by the nature of the stimulus that acts on

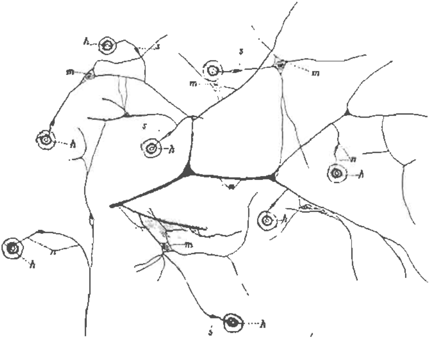

Fig. 146.—Surface view of subhypodermal nerves and nerve-cells from the silkworm (From Hilton)

each. This stimulus may be either a mechanical stimulus, a chemical one, or light. The organs of touch and of hearing respond to mechanical stimuli; the former, to simple contact with other objects; the latter, to vibratory motion caused by waves of sound. The organs of taste and of smell are influenced only by soluble substances and it seems probable that chemical changes are set up in the sense-cells by these substances; hence these organs are commonly referred to as the chemical sense-organs; no criterion has been discovered by which the organs of taste and of smell in insects can be distinguished. The organs of sight are acted upon by light; it is possible that the action of light in this case is a chemical one, as it is on a photographic plate,

but the eyes have not been classed among the chemical sense-organs. For these reasons the following groups of sense-organs are recognized:

The mechanical sense-organs.—The organs of touch and of hearing.

The chemical sense-organs.—The organs of taste and of smell.

The organs of sight.—The compound eyes and the ocelli.

The cuticular part of the sense-organs.—In most if not all of the sense-organs of insects there exists one or more parts that are of cuticular formation. The cuticular parts of the organs of sight and of hearing are described later, in the accounts of these organs; in this place, a few of the modifications of the cuticula found in other sense-organs are described.

Each of the cuticular formations described here is found either within or at the outer end of a pore in the cuticula; as some of these formations are obviously setæ and others are regarded as modified setæ, this pore is usually termed the *trichopore*; it has also been termed the *neuropore*, as it is penetrated by a nerve-ending.

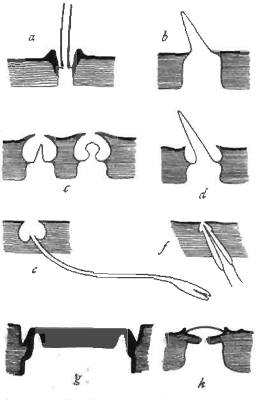

Fig. 147.—Various forms of the cuticular portion of the setiferous sense-organs. The lettering is explained in the text.

As the cuticular part of this group of sense-organs, those other than the organs of hearing and of sight, is regarded as a seta, more or less modified, these organs are often referred to as the *setiferous sense-organs;* they are termed the *Hautsinnesorgane* by German writers.

Special terms have been applied to the different types of setiferous sense-organs, based on the form of the cuticular part of each; but these types cannot be sharply differentiated as intergrades exist between them. In Figure 147 are represented the cuticular parts of several of these different types; these are designated as follows:

The thick-walled sense-hair, sensillum trichodeum.—In this type the cuticular part is a seta, the base of which is in an alveolus at the end of a trichopore and is connected with the wall of the trichopore by a thin articular membrane (Fig. 147, *a*.)

If the sense-hair is short and stout, it is termed by some writers a *sense-bristle, sensillum chæticum;* but there is little use for this distinction.

In the thick-walled sense-hairs, the wall of the seta is fitted to receive only mechanical stimuli, being relatively thick, and as these organs lack the characteristic features of the organs of hearing, they are believed to be organs of touch.

The sense-cones.—The sense-cones vary greatly in form and in their relation to the cuticula of the body-wall; their distinctive feature is that they are thin-walled. For this reason, they are believed to be chemical sense-organs, the thinness of the wall of the cone permitting osmosis to take place through it. In the sense-cones, too, there is no joint at the base, as in the sense-hairs, the articular membrane being of the same thickness as the wall of the cone; there is, therefore, no provision for movement in response to mechanical stimuli.

In one type of sense-cone, the *sensillum basiconicum*, the base of the cone is at the surface of the body-wall (Fig. 147, *b*). In another type, *sensillum cœloconicum*, the cone is in a pit in the cuticula of the body-wall (Fig. 147, *c*). Two forms of this type are represented in the figure; in one, the sense-cone is conical; in the other, it is fungiform. Intergrades between the basiconicum and the cœloconicum types exist (Fig. 147, *d*).

The flask-like sense-organ, sensillum ampullaceum.—This is a modification of the sense-cone type, the characteristic feature of which is that the cone is at the bottom of an invagination of the articular membrane; in some cases the invagination is very deep so that the cone is far within the body-wall (Fig. 147, *e*); intergrades between this form and the more common *sensillum cœloconicum* exist (Fig. 147, *f*).

The pore-plate, sensillum placodeum.—In this type the cuticular part of the organ is a plate closing the opening of the trichopore; in some cases, this plate is of considerable thickness with a thin articular membrane (Fig. 147, *g*); in others it is thin throughout (Fig. 147, *h*).

The olfactory pores.—This type of sense-organ is described later.

X. THE ORGANS OF TOUCH

The organs of touch are the simplest of the organs of special sense of insects. They are widely distributed over the surface of the body and of its appendages. Each consists of a seta, with all the characteristics of setæ already described, a trichogen cell, which excreted the

seta, and a bipolar nerve-cell. These organs are of the type known as *sensillum trichodeum* referred to in the preceding section of this chapter.

According to the observations of Hilton ('02) the terminal prolongation of the nerve-cell enters the hair and ends on one side of it at some distance from its base (Fig. 148). The proximal part of this nerve-cell is connected with the peripheral sensory nervous system, as already described (page 128).

The presence of this nervous connection is believed to distinguish tactile hairs from those termed clothing hairs, and from the scales that are modified setæ. If this distinction is a good one, it is quite probable that many hairs and scales that are now regarded as merely clothing will be found to be sense-organs, when studied by improved histological methods. In fact Guenther ('01) and others have shown that some of the scales on the wings of Lepidoptera, especially those on the veins of the wings, are supplied with nerves; but the function of these scales is unknown.

Hilton states that he "found no evidence to indicate nerves ending in gland cells or trichogen cells by such branches as have been described and figured by Blanc ('90), but in every case the very fine nerve termination could be traced up past the hypodermal cell layer with no branches." Many figures of unbranched nerve fibers ending in sense-hairs are also given by O. vom Rath ('96).

A very different form of nerve-endings in sense-hairs is given by Berlese ('09, *a*). This author represents the nerve extending to a sense-hair as dividing into many bipolar nerve-endings.

XI. THE ORGANS OF TASTE AND OF SMELL

(*The chemical sense-organs*)

It is necessary to discuss together the organs of taste and of smell, as no morphological distinction between them has been discovered. If a chemical sense-organ is so located that it comes in contact with the food of the insect, it is commonly regarded as an organ of taste, if not so situated, it is thought to be an organ of smell. In the present state of our knowledge, this is the only distinction that can be made between these two kinds of organs.

Many experiments have been made to determine the function of the various chemical sense-organs but the results are, as yet, far from conclusive. The problem is made difficult by the fact that these

organs are widely distributed over the body and its appendages, and in some parts, as on the antennæ of many insects, several different types of sense-organs are closely associated.

Those organs that are characterized by the presence of a thin-walled sense-cone (Fig. 147, *b-f*) or by a pore-plate (Fig. 147, *g*, *h*) are believed to be chemical sense-organs. It is maintained by Berlese ('09, *a*) that an essential feature of these chemical sense-organs is the presence of a gland-cell, the excretion of which, passing through the thin wall of the cuticular part, keeps the outer surface of this part, the sense-cone or pore-plate, moist and thus fitted for the reception of chemical stimuli. According to this view a chemical sense-organ consists of a cuticular part, a trichogen cell or cells which produced

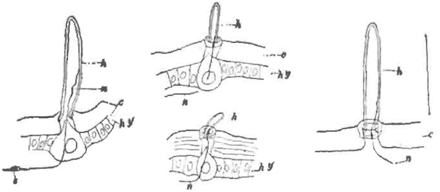

Fig. 148.—Sections through the body-wall and sense-hairs of the silkworm: *c*, cuticula; *h*, hair; *hy*, hypodermis; *n*, nerve; *s*, bipolar nerve-cell (From Hilton). The line at the right of the figure indicates one tenth millimeter.

this part, a gland-cell which excretes a fluid which keeps the part moist, and a nerve-ending.

It is interesting to note that tactile hairs may be regarded as specialized clothing hairs, specialized by the addition of a nervous connection, and that sense-cones and pore-plates may be regarded as specialized glandular hairs with a nervous connection; in the latter case, the specialization involves a thinning of the wall of the hair so as to permit of osmosis through it.

In the different accounts of chemical sense-organs there are marked differences as regards the form of the nerve-endings. In many of the descriptions and figures of these organs the nerve-ending is represented as extending unbranched to the chitinous part of the organ, resembling in this respect those represented in Figure 148. In other accounts the gland-cell is surrounded by an involucre of nerve-cells (Fig. 149).

In the types of chemical sense-organs described above the action of the chemical stimuli is supposed to be dependent upon osmosis through a delicate cuticular membrane. It should be noted, however, that several writers have described sense-cones in which there is a pore; but the accuracy of these observations is doubted by other writers.

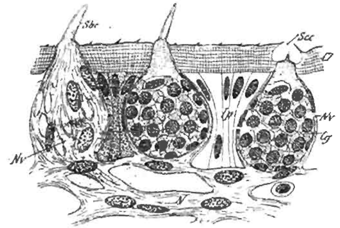

Fig. 149.—Section of the external layers of the wall of an antenna of *Acrida turrita*: *Ct*, cuticula; *Ip*, hypodermis; *N*, nerve; *Nv*, involucre of nerve-cells surrounding the glandular part of a sense-organ; *Sbc*, sensillum basiconicum; *Scc*, sensillum cœloconicum. Three sense-organs are figured; a surface view of the first is represented, the other two are shown in section. (From Berlese).

A very different type of sense-organs which has been termed *olfactory pores* is described in the concluding section of this Chapter.

XII. THE ORGANS OF SIGHT

a. THE GENERAL FEATURES

The two types of eyes of insects.—It is shown in the preceding chapter that insects possess two types of eyes, the ocelli or simple eyes and the compound or facetted eyes.

Typically both types of eyes are present in the same insect, but either may be wanting. Thus many adult insects lack ocelli, while the larvæ of insects with a complete metamorphosis (except *Corethra*) lack compound eyes.

When all are present there are two compound eyes and, typically, two pairs of ocelli; but almost invariably the members of one pair of ocelli are united and form a single median ocellus. The median ocellus is wanting in many insects that possess the other two ocelli.

The distinction between ocelli and compound eyes.—The most obvious distinction between ocelli and compound eyes is the fact that in an ocellus there is a single cornea while in a compound eye there are *many*. Other features of compound eyes have been regarded as distinctively characteristic of them; but in the case of each of these features it is found that they exist in some ocelli.

Each ommatidium of a compound eye has been considered as a separate eye because its nerve-endings constituting the retinula are isolated from the retinulæ of other ommatidia by surrounding accessory pigment cells; but a similar isolation of retinulæ exist in some ocelli.

It has also been held that in compound eyes there is a layer of cells between the corneal hypodermis and the retina, the crystalline-cone-cells, which is absent in ocelli; but in the ocelli of adult Ephemerida there is a layer of cells between the lens and the retina, which, at least, is in a position analogous to that of the crystalline-cone-cells; the two may have had a different origin, but regarding this, we have, as yet, no conclusive data.

The absence of compound eyes in most of the Apterygota.—Typically insects possess both ocelli and compound eyes; when either kind of eyes is wanting it is evidently due to a loss of these organs and not to a generalized condition. Although compound eyes are almost universally absent in the Apterygota in the few cases where they are present in this group they are of a highly developed type and not rudimentary; the compound eyes of *Machilis*, for example, are as perfect as those of winged insects.

The absence of compound eyes in larvæ.—The absence of compound eyes in larvæ is evidently a secondary adaptation to their particular mode of life, like the internal development of wings in the same forms. In the case of the compound eyes of larvæ, the development of the organs is retarded, taking place in the pupal stage instead of in an embryonic stage, as is the case with nymphs and naiads.

While the development of the compound eyes as a whole is retarded in larvæ, a few ommatidia may be developed and function as ocelli during larval life.

b. THE OCELLI

There are two classes of ocelli found in insects: first, the ocelli of adult insects and of nymphs and naiads, which may be termed the *primary ocelli;* and second, the ocelli of most larvæ possessing ocelli, which may be termed *adaptive ocelli.*

The primary ocelli.—The ocelli of adult insects and of nymphs and naiads having been originally developed as ocelli are termed the primary ocelli. Of these there are typically two pairs; but usually when they are present there are only three of them, and in many cases only a single pair.

When there are three ocelli, the double nature of the median ocellus is shown by the fact that the root of the nerve is double, while that of each of the other two is single.

In certain generalized insects, as some Plecoptera, (Fig. 150) all of the ocelli are situated in the front; but in most insects, the paired *ocelli have either migrated into the suture between the front and the vertex* (Fig. 151), or *have proceeded farther and are situated in the vertex.*

The structure of primary ocelli is described later.

The adaptive ocelli.—Some larvæ, as those of the Tenthredinidæ, possess a single pair of ocelli, which in their position and in their structure agree with the ocelli of the adult insects; these are doubtless primary ocelli. But most larvæ have lost the primary ocelli; and if they possess ocelli the position of them and their structure differ greatly from the positions and structure of primary ocelli.

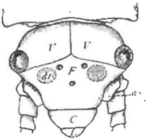

Fig. 150.—Head of a naiad of *Pteronarcys; dt*, spots in the cuticula beneath which the dorsal arms of the tentorium are attached; the three ocelli are on the front (F), between these two spots.

Except in the few cases where primary ocelli have been retained by larvæ, the ocelli of larvæ are situated in a position corresponding to the position of the compound eyes of the adult (Fig. 152); and there are frequently several of these ocelli on each side of the head. This has led to the belief that they represent a few degenerate ommatidia, which have been retained by the larva, while the development of the greater number of ommatidia has been retarded. For this reason they are termed *adaptive ocelli.*

The number of adaptive ocelli varies greatly, and sometimes is not constant in a species; thus in the larva of *Corydalus*, there may be either six or seven ocelli on each side of the head.

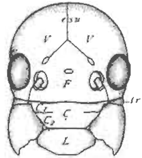

Fig. 151.—Head of a cricket.

There are also great variations in the structure of adaptive ocelli. These variations probably represent different degrees of degeneration or of retardation of development. The extreme of simplicity is found in certain dipterous larvæ; according to Hesse ('01) an ocellus of *Ceratopogon* consists of only two sense-cells. As examples of complicated adaptive ocelli, those of lepidopterous larvæ can be cited.

The ocellus of *Gastropacha rubi*, which is described and figured by Pankrath ('90), resembles in structure, to a remarkable degree, an ommatidium, and the same is true of the ocellus of the larva of *Arctia caja* figured by Hesse ('01).

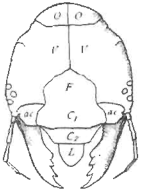

Fig. 152.—Head of a larva of *Corydalus*, dorsal aspect.

The structure of a visual cell.—The distinctively characteristic feature of eyes is the presence of what is termed *visual cells*. In insects, and in other arthropods, a visual cell is a nerve-end-cell, which contains a nucleus and a greater or less amount of pigment, and bears a characteristic border, termed the *rhabdomere;* this is so called because it forms a part of a rhabdom.

The visual cells are grouped in such a way that the rhabdomeres of two or more of them are united to form what is known as a *rhabdom* or optic rod. A group of two visual cells with the rhabdom formed by their united rhabdomeres is shown in Figure 153, A and B.

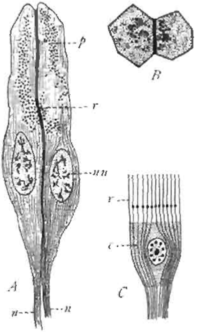

Fig. 153.—Two visual cells from an ocellus of a pupa of *Apis mellifica*. A, longitudinal section; B, transverse section; *n*, *n*, nerves; *nu*, nucleus; *r*, rhabdom; *p*, pigment (After Redikorzew), C, diagram illustrating the structure of a rhabdomere; *r*, rhabdomere; *c*, cell-body (From Berlese after Hesse).

The form of the rhabdomere varies greatly in the visual cells of different insect eyes; and the number of rhabdomeres that enter into the composition of a rhabdom also varies.

Figure 153, C represents in a diagrammatic manner the structure of rhabdomere as described by Hesse ('01). The rhabdomere (r) consists of many minute rodlets each with a minute knob at its base and connected with a nerve fibril.

The structure of a primary ocellus.—The primary ocelli vary greatly in the details of the form of their parts, but the essential features of their structure are illustrated by the accompanying diagram (Fig. 154).

In some ocelli, as for example the lateral ocelli of scorpions, the visual cells are interpolated among ordinary hypodermal cells,

the two kinds forming a single layer of cells beneath the cornea; but in the ocelli of insects, the sense-cells form a distinct layer beneath the hypodermal cells. In this type of ocellus the following parts can be distinguished:

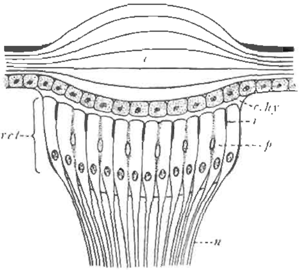

Fig. 154.—A diagram illustrating the structure of a primary ocellus; *c*, cornea; *c. hy*, corneal hypodermis; *ret*, retina; *n*, ocellar nerve; *p*, accessory pigment cell; *r*, rhabdom.

The cornea.—The cornea (Fig. 154, *c*) is a transparent portion of the cuticula of the body-wall; this may be lenticular in form or not.

The corneal hypodermis.—The hypodermis of the body-wall is continued beneath the cornea (Fig. 154, *c. hy.*): this part of the hypodermis is termed by many writers the *vitreous layer* of the ocellus; but the term *corneal hypodermis*, being a self-explanatory term, is preferable. Other terms have been applied to it, as the *lentigen layer* and the *corneagen*, both referring to the fact that this part of the hypodermis produces the cornea.

The retina.—Beneath the corneal hypodermis is a second cellular layer, which is termed the *retina*, being composed chiefly or entirely of visual cells (Fig. 154, ret).

The visual cells of the retina are grouped, as described above (Fig. 153), so that the rhabdomeres of several of them, two, three or four, unite to form a rhabdom; such a group of retinal cells is termed a *retinula*.

The visual cells are nerve-end-cells, each constituting the termination of a fiber of the ocellar nerve, and are thus connected with the central nervous system.

Accessory pigment cells.—In some ocelli there are densely pigmented cells between the retinulæ, which serve to isolate them in a similar way to that in which the retinula of an ommatidium of a compound eye is isolated (Fig. 154, *p*). Even in cases where accessory pigment cells are wanting a degree of isolation of the rhabdoms of the retinulæ of an ocellus is secured by pigment within the visual cells (Fig. 153, *p*).

Ocelli of Ephemerida.—It has been found that the ocelli of certain adult Ephemerida differ remarkably from the more common type of ocelli described above. These peculiar ocelli have been described and figured by Hesse ('01) and Seiler ('05). In them the cuticula over the ocellus, the cornea, is arched but not thickened and the corneal hypodermis is a thin layer of cells immediately beneath it. Under the hypodermis there is a lens-shaped mass of large polygonal cells; and between this lens and the retina there is a layer of closely crowded columnar cells.

The development of these ocelli has not been studied; hence the origin of the lens-shaped mass of cells and of the layer of cells between it and the retina is not known.

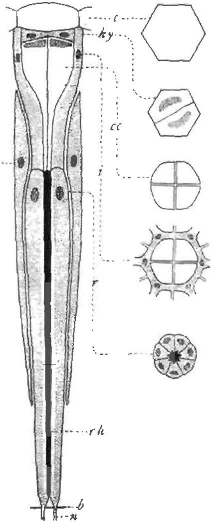

Fig. 155.—An ommatidium of *Machilis*. The lettering is explained in the text.

c. THE COMPOUND EYES

A compound eye consists of many quite distinct elements, the ommatidia, each represented externally by one of the many facets of which the cuticular layer of the eye is composed. As the ommatidia of a given eye are similar, a description of the structure of one will serve to illustrate the structure of the eye as a whole.

The structure of an ommatidium.—The compound eyes of different insects vary in the details of their structure; but these variations are merely modifications of a common plan; this plan is well-illustrated by the compound eyes of *Machilis*, the structure of which was worked out by Seaton ('03). Figure 155 represents a longitudinal section and a series of transverse sections of an ommatidium in an eye of this insect, which consists of the following parts.

The cornea.—The cornea is a hexagonal portion of the cuticular layer of the eye and is biconvex in form (Fig. 155, *c*).

The corneal hypodermis.—Beneath each facet of the cuticular layer of the eye are two hypodermal cells

which constitute the corneal hypodermis of the ommatidium. These cells are quite distinct in *Machilis* and their nuclei are prominent (Fig. 155, *hy*); but in many insects they are greatly reduced, and consequently are not represented in many of the published figures of compound eyes.

The crystalline-cone-cells.—Next to the corneal hypodermis there are four cells, which in one type of compound eyes, the eucone eyes, form a body known as the crystalline-cone, for this reason these cells are termed the *crystalline-cone-cells* (Fig. 155, *cc*). Two of these cells are represented in the figure of a longitudinal section and all four, in that of a transverse section. In each cell there is a prominent nucleus at its distal end.

The iris-pigment-cells.—Surrounding the crystalline-cone-cells and the corneal hypodermis, there is a curtain of densely pigmented cells, which serves to exclude from the cone light entering other ommatidia; for this reason these cells are termed the *iris-pigment* (Fig. 155, *i*). They are also known as the *distal retinula cells;* but as they are not a part of the retina this term is misleading.

There are six iris-pigment-cells surrounding each crystalline-cone; but as each of these cells forms a part of the iris of three adjacent ommatidia, there are only twice as many of these cells as there are ommatidia. This is indicated in the diagram of a transverse section (Fig. 155, *i*).

The retinula.—At the base of each ommatidium, there is a group of visual cells forming a retinula (Fig. 155, *r*); of these there are seven in *Machilis;* but they vary in number in the eyes of different insects. The visual cells are so grouped that their united rhabdomeres form a rhabdom, which extends along the longitudinal axis of the ommatidium (Fig. 155, *rh*). The distal end of the rhabdom abuts against the proximal end of the crystalline-cone; and the nerve-fibers of which the visual cells are the endings pass through the basement membrane (Fig. 155, *b*) to the optic nerve.

The visual cells are pigmented and thus aid in the isolation of the ommatidium.

The accessory pigment-cells.—In addition to the two kinds of pigment-cells described above there is a variable number of accessory pigment-cells (Fig. 155, *ap*), which lie outside of and overlap them.

From the above it will be seen that each ommatidium of a eucone eye is composed of five kinds of cells, three of which, the corneal hypodermis, the crystalline-cone-cells, and the retinular cells produce solid structures; and three of them are pigmented.

Three types of compound eyes are recognized: first, the *eucone eyes*, in these each ommatidium contains a true crystalline-cone, as described above, and the nuclei of the cone-cells are in front of the cone; second, the *pseudocone eyes*, in these the four cone-cells are filled with a transparent fluid medium, and the nuclei of these cells are behind the refracting body; and third, the *acone eyes*, in which although the four cone-cells are present they do not form a cone, either solid or liquid.

d. THE PHYSIOLOGY OF COMPOUND EYES

The compound eyes of insects and of crustacea are the most complicated organs of vision known to us. It is not strange therefore, that the manner in which they function has been the subject of much discussion. It is now, however, comparatively well-understood; although much remains to be determined.

In studying the physiology of compound eyes, three sets of structures, found in each ommatidium, are to be considered: first, the dioptric apparatus, consisting of the cornea and the crystalline-cone; second, the percipient portion, the retinula, and especially the rhabdom; and third, the envelope of pigment, which is found in three sets of cells, the iris-pigment-cells, the retinular cells, and the accessory or secondary pigment-cells.

The dioptrics of compound eyes is an exceedingly complicated subject; a discussion of it would require too much space to be introduced here. It has been quite fully treated by Exner ('91), to whose work those especially interested in this subject are referred. The important point for our present discussion is that by means of the cornea and the crystalline-cone, light entering the cornea from within the limits of a certain angle passes through the cornea and the crystalline-cone to the rhabdom, which is formed of the combined rhabdomeres of the nerve-end-cells, constituting the retinula, the precipient portion of the ommatidium.

The theory of mosaic vision.—The first two questions suggested by a study of physiology of compound eyes have reference to the nature of the vision of such an eye. What kind of an image is thrown upon the retinula of each ommatidium? And how are these images combined to form the image perceived by the insect? Does an insect with a thousand ommatidia perceive a thousand images of the object viewed or only one?

The theory of mosaic vision gives the answers to these questions. This theory was proposed by J. Müller in 1826; and the most recent

investigations confirm it. The essential features of it are the following: only the rays of light that pass through the cornea and the crystalline-cones reach the precipient portion of the eye, the others fall on the pigment of the eye and are ahsorbed by it; in each ommatidium the cornea transmits to the crystalline-cone light from a very limited field of vision, and when this light reaches the apex of the crystalline-cone it forms a point of light, not an image; hence the image formed upon the combined retinulæ is a mosaic of points of light, which combined make a single image, and this image is an erect one.

Figure 156 will serve to illustrate the mosaic theory of vision. In this figure are represented the corneas (*c*), the crystalline-cones (*cc*), and the rhabdoms (*r*.) of several adjacent ommatidia. It can be seen, from this diagram, that each rhabdom receives a point of light which comes from a limited portion of the object viewed (O); and that the image (I) received by the percipient portion of the eye is a single erect image, formed by points of light, each of which corresponds in density and color to the corresponding part of the object viewed.

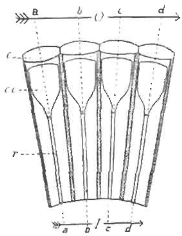

Fig. 156.—Diagram illustrating the theory of mosaic vision.

The distinctness of vision of a compound eye depends in part upon the number and size of the ommatidia. It can be readily seen that the image formed by many small ommatidia will represent the details of the object better than one formed by a smaller number of larger ommatidia; the smaller the portion of the object viewed by each ommatidium the more detailed will be the image.

The distinctness of the vision of a compound eye depends also on the degree of isolation of the light received by each ommatidium, which is determined by the amount and distribution of the pigment. Two types of compound eyes, differing in the degree of isolation of the light received by each ommatidium, are recognized; to one type has been applied the term day-eyes, and to the other, night-eyes.

Day-eyes.—The type of eyes known as day-eyes are so-called because they are fitted for use in the day-time, when there is an abundance of light. In these eyes the envelope of pigment surrounding the transparent parts of each ommatidium is so complete that only the light that has traversed the cornea and crystalline-cone

of that ommatidium reaches its rhabdom. The image formed in such an eye is termed by Exner an *apposed image;* because it is formed by apposed points of light, falling side by side and not overlapping. Such an image is a distinct one.

Night-eyes.—In the night-eyes the envelope of pigment surrounding the transparent parts of each ommatidium is incomplete; so that rays of light entering several adjacent corneas can reach the same retinula. In such an eye there will be an overlapping of the points of light; the image thus formed is termed by Exner a *superimposed image.* It is obvious that such an image is not as distinct as an apposed image. It is also obvious that a limited amount of light will produce a greater impression in this type of eye than in one where a considerable part of the light is absorbed by pigment. Night-eyes are fitted to perceive objects and the movement of objects in a dim light, but only the more general features of the object can be perceived by them.

Eyes with double function.—It is a remarkable fact that with many insects and crustacea the compound eyes function in a bright light as day-eyes and in a dim light as night-eyes. This is brought about by movements in the pigment. If an insect having eyes of this kind be kept in a light place for a time and then killed while still in the light, its eyes will be found to be day-eyes, that is eyes fitted to form apposed images. But if another insect of the same species be kept in a dark place for a time and then killed while still in the dark, its eyes will be found to be night-eyes, that is eyes fitted to form superimposed images.

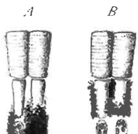

Fig. 157.—Ommatidia from eyes of *Colymbetes;* A, day-eye condition; B, night-eye condition (From Exner).

Figure 157 represents two preparations showing the structure of the compound eyes of a diving-beetle, studied by Exner. In one (Fig. 157, *A*), each rhabdom is surrounded by an envelope of pigment, so that it can receive only the light passing through the crystalline-cone of the ommatidium of which this rhabdom is a part. This is the condition found in the individual killed in the light, and illustrates well the structure of a day-eye. In the other preparation (Fig. 157, *B*), which is from an individual killed in the dark, it can be seen that the pigment has moved up between the crystalline-cones so that

the light passing from the tip of a cone may reach several rhabdoms, making the eye a night-eye. These changes in the position of the pigment are probably due to amœboid movements of the cells.

Divided Eyes.—In many insects each compound eye is divided into two parts; one of which is a day-eye, and the other a night-eye. The two parts of such an eye can be readily distinguished by a difference in the size of the facets; the portion of the eye that functions as a day-eye being composed of much smaller facets than that which functions as a night-eye.

A study of the internal structure of a divided eye shows that the distribution of the pigment in the part composed of smaller facets is that characteristic of day-eyes; while the part of the eye composed of larger facets is fitted to produce a superimposed image, which is the distinctive characteristic of night-eyes.

Great differences exist in the extent to which the two parts of a divided eye are separated. In many dragon-flies the facets of a part of each compound eye are small, while those of the remainder of the eye are much larger; but the two fields are not sharply separated. In some *Blepharocera* the two fields are separated by a narrow band in which there are no facets, and the difference in the size of the facets of the two areas is very marked. The extreme condition is reached in certain May-flies, where the two parts of the eye are so widely separated that the insect appears to have two pairs of compound eyes (Fig 158).

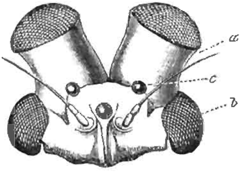

Fig. 158.—Front of head of Cloëon, showing divided eyes; *a*, night-eye; *b*, day eye; *c*, ocellus (From Sharp).

The tapetum.—In the eyes of many animals there is a structure that reflects back the light that has entered the eye, causing the well-known shining of the eyes in the dark. This is often observed in the eyes of cats and in the eyes of moths that are attracted to our light at night. The part of the eye that causes this reflection is termed a *tapetum*. The supposed function of a tapetum is to increase the effect of a faint light, the light being caused to pass through the retina a second time, when it is reflected from the tapetum.

The structure of the tapetum varies greatly in different animals; in the cat and other carnivores it is a thick layer of wavy fibrous tissue; in spiders it consists of a layer of cells behind the retina containing

small crystals that reflect the light; and in insects it is a mass of fine tracheæ surrounding the retinula of each ommatidium.

XIII. THE ORGANS OF HEARING

a. THE GENERAL FEATURES

The fact that in many insects there are highly specialized organs for the production of sounds indicates that insects possess also organs of hearing; but in only a few cases are these organs of such form that they have been generally recognized as ears.

Fig. 159.—Side view of a locust with the wings removed; *t*, tympanum.

The tympana.—In most of the jumping Orthoptera there are thinned portions of the cuticula, which are of a structure fitted to be put in vibration by waves of sound. For this reason these have been commonly regarded as organs of hearing, and have been termed *tympana*. In the Acridiidæ, there is a tympanum on each side of the first abdominal segment (Fig. 159); and in the Locustidæ and in the Gryllidæ, there is a pair of tympana near the proximal end of each tibia of the first pair of legs (Fig. 160).

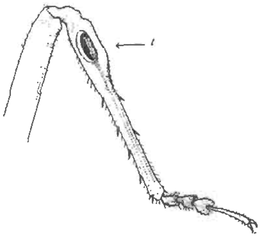

Fig. 160.—Fore leg of a katydid; *t*, tympanum.

The chordotonal organs.—An ear to be effective must consist of something more than a membrane that will be put in vibration by means of sound; the vibrations of such a tympanum must be transferred in some way to a nervous structure that will be influenced by them if the sound is to be perceived. Such structures, closely associated with the tympana of Orthoptera, were discovered more than a half century ago by Von Siebold (1844) and have been studied since by many investigators. The morphological unit of these essential auditory

structures of insects is a more or less peg-like rod contained in a tubular nerve-ending (Fig. 161, A and B); this nerve-ending may or may not be associated with a specialized tympanum. To all sense-organs characterized by the presence of these auditory pegs, Graber ('82) applied the term *chordotonal organs* or fiddle-string-like organs.

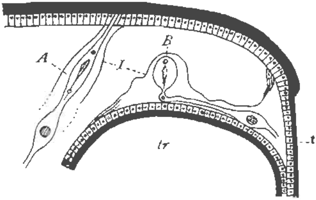

Fig. 161.—Diagrammatic representation of the auditory organs of a locustid (After Graber).

The scolopale and the scolopophore.—The peg-like rod characteristic of a chordotonal organ of an insect was named by Graber the *scolopale;* and to the tubular nerve-ending containing the scolopale, he applied the term *scolopophore.*

Fig. 162.—A scolopophore of the integumental type (From Hess).

The integumental and the subintegumental scolopophores.—With respect to their position there are two types of scolopophores; in one, the nerve-ending is attached to the body-wall (Fig. 161, A); in the other, it ends free in the body-cavity (Fig. 161, B). These two types are designated respectively as *integumental scolopophores* and *subintegumental scolopophores.*

The structure of a scolopophore.—In a scolopophore there can be distinguished an outer sheath (Fig. 161, I), which appears to be continuous either with the basement membrane of the hypodermis or with that of the epithelium of a trachea, and within this sheath the complicated nerve-ending; this nerve-ending is represented diagrammatically in Figure 161 from Graber and in detail in Figure 162 from Hess ('17).

In Figure 162 the following parts are represented: a bipolar sense-cell (*sc*) with its nucleus (scn); the proximal pole of this sense-cell is connected with the central nervous system by a nerve; and its distal pole is connected with the scolopale (*s*) by an axis-fiber (*af*); surrounding the distal prolongation of the sense-cell and the scolopale there is an enveloping or accessory cell (*ec*), in which there is a prominent nucleus (*ecn*); distad of the enveloping cell is

the cap-cell (*cc*), in which there is a nucleus (*ccn*); extending from the end-knob (*ek*) of the scolopale and surrounded by the cap-cell there is an attachment fiber or terminal ligament (*tl*), by which the scolopophore is attached to the body-wall, the scolopophore represented being of the integumental type; at the base of the scolopale and partly surrounding it, there is a vacuole (*v*).

The structure of a scolopale.—The scolopalæ or auditory pegs are exceedingly minute and are quite uniform in size, regardless of the size of the insect in which they are; but they vary in form in different insects. They are hollow (Fig. 162, *s*); but the wall of the scolopale is almost always thickened at its distal end, this forming an end-knob (Fig. 162, *ek*). They are traversed by the axis-fiber of the sense-cell. The vacuole at the base of the scolopale connects with the lumen of the scolopale; this vacuole is filled with watery fluid.

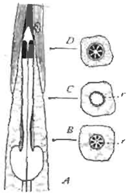

Fig. 163.—Part of the scolopophore shown in Figure 162 more enlarged (From Hess).

In Figure 163 is shown a part of the scolopophore represented in Figure 162, more enlarged (A), and three cross-sections (B, C, D) of the scolopale. The wall of the scolopale is composed at either end of seven ribs (*r*), each of which is divided in the central portion, making fourteen ribs in this part. The entire scolopale, except possibly the terminal ligament, is bathed in the watery liquid, and is free to vibrate (Hess '17).

It should be remembered that the scolopalæ of different insects vary greatly in form; the one figured here is merely given as an example of one type.

The simpler forms of chordotonal organs.—In the simplest form of a chordotonal organ there is a single scolopophore; usually, however, there are two or more closely parallel scolopophores. In figure 164, which represents a chordotonal organ found in the next to the last segment of the body of a larva of *Chironomus*, these two types are represented, one part of the organ being composed of a single scolopophore, the other of several.

The chordotonal ligament.—In Figure 164 the nerve connecting the chordotonal organ with the central nervous system is represented at *n*; and at *li* is shown a structure not yet mentioned, the *chordotonal ligament*, which is found in many chordotonal organs. Figure 165 is a diagrammatic representation of the relations of the chordotonal organs of a larva of *Chironomus* to the central nervous system

and to the body-wall. Here each chordotonal organ is approximately T-shaped; the proximal nerve forming the body of the T; the scolopophore, one arm; and the chordotonal ligament, the other arm.

It will be observed that in this type of chordotonal organ the scolopophore and the ligament form a fiddle-string-like structure between two points in the wall of a single segment. It is believed that in cases of this kind the integument acts as a tympanum or sounding board.

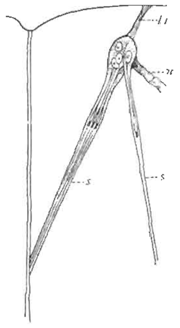

Fig. 164.—Chordotonal organ of a larva of *Chironomus* (From Graber).

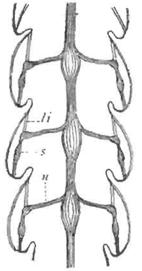

Fig. 165.—Diagram representing the chordotonal organs of a larva of *Chironomus* (After Graber).

b. THE CHORDOTONAL ORGANS OF LARVÆ

Chordotonal organs have been observed in so many larvæ that we may infer that they are commonly present in larvæ. These organs are very simple compared with those of certain adult insects, described later. Those figured in the preceding paragraphs will serve to illustrate the typical form of larval chordotonal organs. Even in the more complicated ones, there are comparatively few scolopophores; and, as a rule, they are not connected with specialized tympana, but extend between distant parts of the body-wall, which probably acts as a sounding board.

In certain larvæ, however, the scolopopbores are attached to specialized areas of the body-wall. Hess ('17) has shown that the pleural discs of cerambycid larvæ, which are situated one on each side of several of the abdominal segments, serve as points of attachment of scolopophores.

c. THE CHORDOTONAL ORGANS OF THE ACRIDIIDÆ

In the Acridiidæ there are highly specialized ears situated one on each side of the first abdominal segment. The external vibrating

part of these organs, the tympanum, is conspicuous, being a thinned portion of the body-wall (Fig. 166).

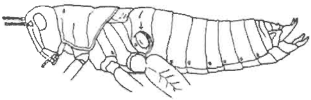

Fig. 166.—Side view of a locust with the wings removed; *t*, tympanum.

Closely applied to the inner surface of each tympanum (Fig. 167, *T*), there is a ganglion known as Muller's organ (*ga*), first described by Muller (1826). This ganglion contains many ganglion-cells and scolopalæ and is the termination of a nerve extending from the central nervous system, the auditory nerve (*n*). Figure 168 represents a section of Müller's organ, showing the ganglion-cells and scolopalæ.

Intimately associated with the Muller's organ are two horny processes (Fig. 167, *o* and *u*) and a pear-shaped vesicle (Fig. 167, *bi*); and near the margin of the tympanum, there is a spiracle (Fig. 167, *st*), which admits air to a space inside of the tympanum, the *tympanal air-chamber*.

As the nerve-endings in Muller's organ are attached to the tympanum, it is a chordotonal organ of the integumental type; it is attached to a vibratile membrane, between two air-spaces.

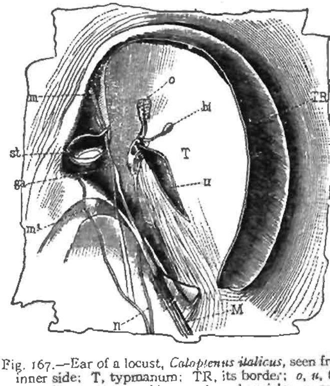

Fig. 167.—Ear of a locust, *Caloptenus italicus*, seen from inner side; T, typmanum; TR, its border; *o*, *u*, two horn-like processes; *bi*, pear-shaped vesicle; *n*, auditory nerve; *ga*, terminal ganglion or Muller's organ; *st*, spiracle; M, tensor muscle of the tympanum (From Packard after Graber).

d. THE CHORDOTONAL ORGANS OF THE LOCUSTIDÆ AND OF THE GRYLLIDÆ

In the long-horned grasshoppers and in the crickets, there is a pair of tympana near the proximal end of the tibia of each fore leg. In

many genera, these tympana are exposed and easily observed (Fig. 169); but in some genera each is covered by a fold of the body-wall and is consequently within a cavity, which communicates with the outside air by an elongated opening (Fig. 170, *a* and *b*).

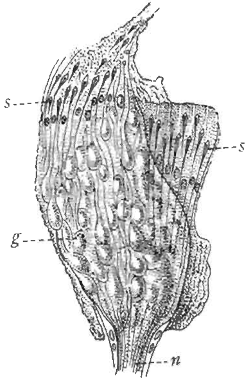

Fig. 168.—Section of Muller's organ: *g*, ganglion-cells; *n*, nerve; *s*, *s*, scolopalæ (After Graber).

Within the legs bearing these tympana, there are complicated chordotonal organs. Very detailed accounts of these organs have been published by Graber ('76), Adelung ('92) and Schwabe ('06); in this place, for lack of space, only their more general features can be described.

Figure 171 represents a longitudinal section of that part of a fore tibia of *Decticus verrucivorus* in which the chordotonal organs are situated, and Figure 172 represents a cross-section of the same tibia, passing through the tympana and the air-chambers formed by the folds of the body-wall. In the following account the references, in most cases, are to both of these figures.

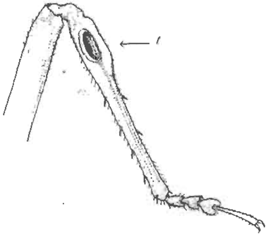

Fig. 169.—Fore leg of a katydid; *t*, tympanum.

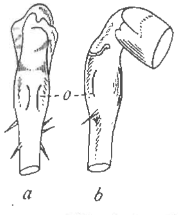

Fig. 170.—Tibia of a locustid with covered tympana; *a*, front view; *b*, side view; *o*, opening (After Schwabe).

The trachea of the leg.—The trachea of the leg figured in part here is remarkable for its great size and for its division into two branches,

the front trachea (Ti) and the hind trachea (Te); these two branches reunite a short distance beyond the end of the chordotonal organs. It is an interesting fact that these large tracheæ of the legs containing the chordotonal organs open through a pair of supernumery spiracles, differing in this respect from the tracheæ of the other legs.

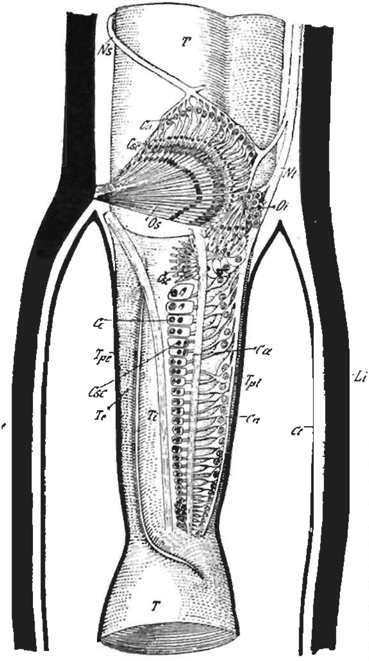

Fig. 171.—Longitudinal section of a fore tibia of *Decticus verrucivorus* (From Berlese after Schwabe).

The spaces of the leg. — By reference to Figure 172, it will be seen that the two branches of the leg trachea occupy the middle space of the leg between the two tympana (Tie and Tii) and separate an outer space, the upper one in the figure, from an inner space. The outer space (E) contains a chordotonal organ, of which the scolopale is represented at S; and the inner space contains small tracheæ (t), muscles (m), the tibial nerve (Ntb), and a tendon (Tn). The interstices of the outer and inner spaces are filled with blood. In the outer space some leucocytes and fat-cells (Gr) are represented.

The supra-tympanal or subgenual organ.—In the outer space of the tibia, a short distance above the tympana, there is a ganglion (Fig.

171, Os) composed of nerve-endings, which are scolopophores of the integumental type. Two nerves extend to this ganglion, one from each side of the leg, and each divides into many scolopophores. The attachment fibers of the scolopophores converge and are attached to the wall of the leg. Two terms have been applied to this organ, both indicating its position in the leg; one refers to the fact that it is above the tympana, the other, that it is below the knee.

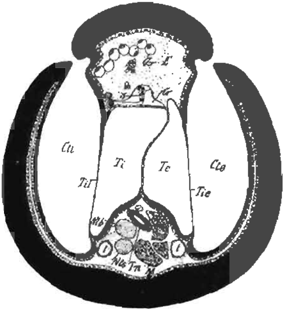

Fig. 172.—Transverse section of the fore tibia of *Decticus verrucivorus* (From Berlese after Schwabe). In comparing this figure with the preceding, note that in that one the external parts are at the left, in this one, at the right.

The intermediate organ.—Immediately below the supra-tympanal organ, and between it and the organ described in the next paragraph, is a ganglion composed of scolopophores of the subintegumental type; this is termed the *intermediate organ* (Fig. 171, Oi).

Siebold's organ or the crista acustica.—On the outer face of the front branch of the large trachea of the leg there is a third chordotonal organ, the *Siebold's organ* or the *crista acusitca*. A surface view of the organ is given in Figure 171 and a cross-section is represented in Figure 172. It consists of a series of scolopophores of the subintegumental type, which diminish in length toward the distal end of the organ (Fig. 171). The relation of Siebold's organ to the trachea is shown in Figure 172. It forms a ridge or crest on the trachea, shown in section at *cr* in Figure 172; this suggested the name *crista acustica*, used by some writers.

e. THE JOHNSTON'S ORGAN

There has been found in the pedicel of the antenna of many insects, representing several of the orders, an organ of hearing, which is known as the *Johnston's organ*, having been pointed out by Christopher Johnston (1855). This organ varies somewhat in form in different

insects and in the two sexes of the same species; but that of a male mosquito will serve as an example illustrating its essential features. The following account is based on an investigation by Professor Ch. M. Child ('94).

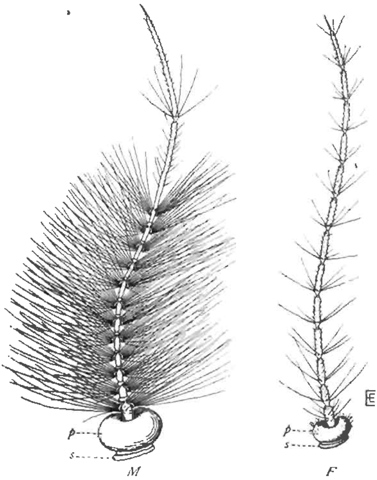

Fig. 173.—Antennæ of mosquitoes, *Culex*: M, male; F, female; *s*, scape; *p*, pedicel.

In an antenna of a mosquito (Fig. 173) the scape or first segment, which contains the muscles of the antenna, is much smaller than the pedicel or second segment, and is usually overlooked, being concealed by the large, globular pedicel; the clavola consists of thirteen slender segments. Excepting one or two terminal segments, each segment of the clavola bears a whorl of long, slender setæ; these are more prominent in the male than in the female.

Figure 174 represents a longitudinal section of the base of an antenna; in this the following parts are shown: S, scape; P, pedicel, C, base of the first segment of the clavola; *cp*, conjunctival plate connecting the pedicel with the first segment of the clavola; *pr*, chitinous processes of the conjunctival plate; *m*, muscles of the antenna; N, principal antennal nerve; *n*, nerve of the clavola; immediately within the wall of the segments there is a thin layer of hypodermis; the lumen of the pedicel is largely occupied by a ganglion composed of scolopophores, the attachment fibers of which are attached to the chitinous processes of the conjunctival plate.

As to the action of the auditory apparatus as a whole, it was shown experimentally by Mayer ('74) that the different whorls of setæ borne by the segments of the clavola, and which gradually decrease in length on successive segments, are caused to vibrate by different notes; and it is believed that the vibrations of the setæ are transferred to the conjunctival plate by the clavola, and thence to the nerve-endings.

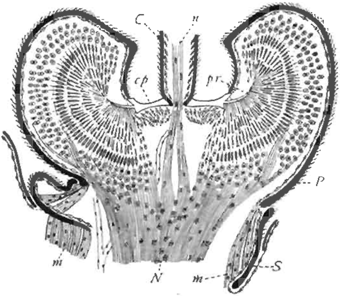

Fig. 174.—Longitudinal section of the base of an antenna of a male mosquito, *Corethra culiciformis* (After Child).

It was formerly believed that the great specialization of the Johnston's organ in male mosquitoes enabled the males to hear the songs of the females and thus more readily to find their mates. But it has been found that in some species, at least, of mosquitoes and of midges in which the males have this organ highly specialized the females seek the males. This has led some writers to doubt that the Johnston's organ is auditory in function. But the fact remains that its distinctive feature is the presence of scolopalæ, which is the distinctive characteristic of the auditory organs of other insects.

XIV. SENSE-ORGANS OF UNKNOWN FUNCTIONS

In addition to the sense-organs discussed in the foregoing account there have been described several types of supposed sense-organs which are as yet very imperfectly understood. Among these there is one that merits a brief discussion here on account of the frequent references to it in entomological literature. Many different names have been applied to the organs of this type; of these that of *sense-domes* is as appropriate as any, unless the conclusions of McIndoo, referred to below, are confirmed, in which case his term *olfactory pores* will be more descriptive.

The sense-domes are found in various situations, but they occur chiefly on the bases of the wings and on the legs. Each sense-dome consists of a thin, hemispherical or more nearly spherical membrane, which either projects from the outer end of a pore in the cuticula (Fig. 175, *a*) or is more or less deeply enclosed in such a pore (Fig. 175, *b*); intergrades between the two types represented in the accompanying figures occur.

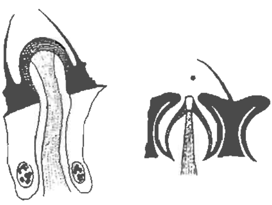

Fig 175.—Sense-domes (From Berlese).

When a sense-dome is viewed in section a nerve-ending is seen to be connected with the dome-shaped or bell-like membrane. A striking feature of these organs is the absence of any gland-cells connected with them, such as are found in the chemical sense-organs described on an earlier page.

In one very important respect there is a marked difference in the accounts of these organs that have been published. The organs were first discovered long ago by Hicks ('57); but they have been more carefully studied in recent years by several writers, who have been able to make use of a greatly improved histological technic; among these writers are Berlese ('09 *a*), Vogel ('11), Hochreuter (12'), Lehr ('14), and McIndoo ('14).

All of the writers mentioned above except the last named maintain that the sense-cell ends in a structure, in the middle of the sense-dome, which differs in appearance from both the membrane of the sense-dome and the body of the sense-cell. This structure varies in form in different sense-domes; in some it is cylindrical, and is consequently described as a peg; in others, it is greatly flattened so that it is semilunar in form when seen in section. In Figure 175, *b*, which represents a section made transversely to the long axis of this part it appears peglike; but in Figure 175, *a*, which represents a longitudinal view of it, it is semilunar in form.

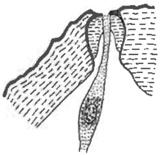

Fig. 176—Olfactory pore of McIndoo (From McIndoo)

According to McIndoo (Fig. 176) no structure of this kind is

present, but the sense-fiber of the sense-cell pierces the bottom of the cone and enters the round, oblong, or slitlike pore-aperture. "It is thus seen that the cytoplasm in the peripheral end of the sense-fiber comes in direct contact with the air containing odorous particles and that odors do not have to pass through a hard membrane in order to stimulate the sense-cell as is claimed for the antennal organs".

XV. THE REPRODUCTIVE ORGANS

a. THE GENERAL FEATURES

In insects the sexes are normally distinct except in a single genus of wingless, very aberrant Diptera, *Termitoxinia*, the members of which live in the nests of Termites; these have been found to be hermaphroditic.

Individuals in which one side has the external characters of the male and the other those of the female are not rare; such an individual is termed a *gynăndromŏrph;* in some gynandromorphs, both testes and ovaries are present but in no case are both functional; these therefore are not true hermaphrodites.

In females the essential reproductive organs consist of a pair of *ovaries*, the organs in which the ova or eggs are developed, and a tube leading from each ovary to an external opening, the *oviduct*. In the male, the essential reproductive organs are a pair of *testes*, in which the spermatozoa are developed and a tube leading from each testis to an external opening, the *vas deferens*. In addition to these essential organs, there are in most insects accessory organs, these consist of glands and of reservoirs for the reproductive elements.

The form of the essential reproductive organs and the number and form of the accessory organs vary greatly in different insects. It is impossible to indicate the extent of these variations in the limited space that can be devoted to this subject in this work. Instead of attempting this it seems more profitable to indicate by diagrams, one for each sex, the relations of the accessory organs that may exist to the essential organs.

In adult insects the external opening of the reproductive organs is on the ventral side of the abdomen near the caudal end of the body. The position of the opening appears to differ in different insects and in some cases in the two sexes of the same species. The lack of uniformity in the published accounts bearing on this point is partly due to differences in numbering the abdominal segments; some authors describing the last segment of the abdomen as the tenth while others

believe it to be the eleventh: embryological evidence supports the latter view.

In most insects there is a single external opening of the reproductive organs; but in the Ephemerida and in a few other insects the two efferent ducts open separately.

Secondary sexual characters.—In addition to differences in the essential reproductive organs and in the genital appendages of the two sexes, many insects exhibit what are termed *secondary sexual characters*. Among the more striking of these are differences in size, coloring, and in the form of certain organs. Female insects are usually larger than the males of the same species; this is due to the fact that the females carry the eggs; but in those cases where the males fight for their mates, as stag-beetles, the males are the larger. Striking differences in the coloring of the two sexes are common, especially in the Lepidoptera. In many insects the antennæ of the male are more highly specialized than those of the female; and this is true also of the eyes of certain insects. These are merely a few of the many known secondary sexual characters found in insects.

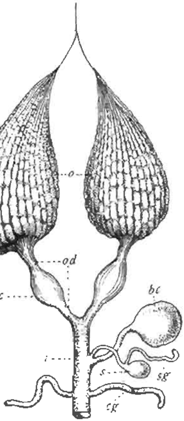

Fig. 177.—Diagram of the reproductive organs of a female insect: *o*, ovary; *od*, oviduct; *c*, egg-calyx; *v*, vagina; *s*, spermatheca; *bc*, bursa copulatrix; *sg*, spermathecal gland; *cg*, colleterial glands.

Fig. 178.—Reproductive organs of *Japyx*, female (After Grassi).

b. THE REPRODUCTIVE ORGANS OF THE FEMALE

The general features of the ovary.—In the more usual form of the ovaries of insects, each ovary is a compact, more or less spindle-shaped body composed of many parallel *ovarian tubes* (Fig. 177, *o*), which open into a common efferent tube, the oviduct. In *Campodea*, however, there is a single ovarian tube; and in certain other Thysanura the ovarian tubes have a metameric arrangement (Fig. 178). The num-

ber of ovarian tubes differs greatly in different insects; in many Lepidoptera there are only four in each ovary; in the honeybee, about 150; and in some Termites, 3000 or more.

The wall of an ovarian tube.—The ovarian tubes are lined with an *epithelial layer*, which is supported by a *basement membrane;* outside of this there is a *peritoneal envelope*, composed of connective tissue; and sometimes there are muscles in the peritoneal envelope.

The zones of an ovarian tube.—Three different sections or zones are recognized in an ovarian tube: first, the *terminal filament*, which is the slender portion which is farthest from the oviduct (Fig. 179, *t*); second, the *germarium*, this is a comparatively short chamber, between the other two zones (Fig. 179, *g*); and third, the *vitellarium*, which constitutes the greater portion of the ovarian tube.

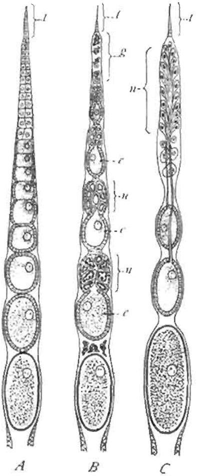

Fig. 179.—Three types of ovarian tubes; *e, e, e,* eggs; *n, n, n,* nurse-cells (After Berlese).

The contents of an ovarian tube.—In the germarium are found the *primordial germ-cells* from which the eggs are developed; and in the vitellarium are found the developing eggs. In addition to the cells that develop into eggs there are found, in the ovarian tubes of many insects, cells whose function is to furnish nutriment to the developing eggs, these are termed *nurse-cells*.

Depending upon the presence or absence of nurse-cells and on the location of the nurse-cells when present, three types of ovarian tubes are recognized: first, those without distinct nurse-cells (Fig. 179, A); second, those in which the eggs and masses of nurse-cells alternate in the ovarian tube (Fig. 179, B); and third, those in which the nurse-cells are restricted to the germarium (Fig. 179, C), which thus becomes a nutritive chamber. In the latter type the developing eggs are each connected by a thread with the nutritive chamber.

The egg-follicles.—The epithelium lining of the ovarian tube becomes invaginated between the eggs in such a way that each egg is

enclosed in an epithelial sac or *egg-follicle*, which passes down the tube with the egg (Fig. 179). There is thus a tendency to strip the tube of its epithelium, but a new one is constantly formed.

The functions of the follicular epithelium.—It is believed that in some cases, and especially where the nurse-cells are wanting, the follicular epithelium serves a nutritive function. But the most obvious function of this epithelium is the formation of the chorion or egg-shell, which is secreted on its inner surface. The pit-like markings so common on the shells of insect eggs indicate the outlines of the cells of the follicular epithelium.

The ligament of the ovary.—In many insects, the terminal filaments of the several ovarian tubes of an ovary unite and form a slender cord, the ligament of the ovary, which is attached to the dorsal diaphragm; but in other insects this ligament is wanting, the terminal filaments ending free in the body cavity.

The oviduct.—The common outlet of the ovarian tubes is the *oviduct* (Fig. 177, *od*). In most insects the oviducts of the two ovaries unite and join a common outlet, the vagina; but in the Ephemerida and in some Dermaptera each oviduct has a separate opening.

The egg-calyx.—In some insects each oviduct is enlarged so as to form a pouch for storing the eggs, these pouches are termed the *egg-calyces* (Fig. 177, c).

The vagina.—The tube into which the oviducts open is the vagina (Fig. 177, *v*). The vagina differs in structure from the oviducts, due to the fact that it is an invagination of the body-wall, and, like other invaginations of the body-wall, is lined with a cuticular layer.

The spermatheca.—The spermatheca is a sac for the storage of the seminal fluid (Fig. 177, *s*). As the pairing of the sexes takes place only once in insects and as the egg-laying period may extend over a long time, it is essential that provision be made for the fertilization of the eggs developed after the union of the sexes. The eggs become full-grown and each is provided with a shell before leaving the ovarian tubes. At the time an egg is laid a spermatozoan may pass from the spermatheca, where thousands of them are stored, into the egg through an opening in the shell, the micropyle, which is described in the next chapter (Fig. 184 and 185).

In some social insects, eggs that are developed years after the pairing took place are fertilized by spermatozoa that have been stored in the spermatheca.

The bursa copulatrix.—In many insects there is a pouch for the reception of the seminal fluid before it passes to the spermatheca.

This pouch is known as the *bursa copulatrix* or copulatory pouch. In some insects this pouch is a diverticulum of the vagina (Fig. 177, *bc*); in others it has a distinct external opening, there being two external openings of the reproductive organs, the opening of the vagina and the opening of the bursa copulatrix.

When the bursa copulatrix has a distinct external opening there may or may not be a passage from it to the vagina. In at least some Orthoptera (*Melanoplus*) there is no connection between the two; when the eggs are laid they are pushed past the opening of the bursa copulatrix where they are fertilized.

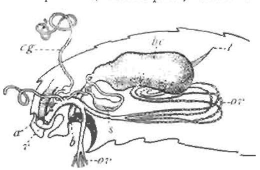

Fig. 180.—Reproductive organs of the female of the milkweed butterfly: *a*, anus; *b*, opening of the bursa copulatrix; *ov*, ovarian tubes; *t*, terminal filaments of the ovary; *v*, opening of the vagina (After Burgess).

In the Lepidoptera (Fig. 180), there is a passage from the bursa copulatrix to the vagina. In this case the seminal fluid is received by the bursa copulatrix at the time of pairing, later it passes to the spermatheca, and from here it passes to the vagina.

A bursa copulatrix is said to be wanting in Hymenoptera, Diptera, Heteroptera and Homoptera except the Cicadas.

The colleterial glands.—There are one or two pairs of glands that open into the vagina near its outlet (Fig. 177, *cg*); to these has been applied the general term *colleterial glands*. Their function differs in different insects; in some insects they secrete a cement for gluing the eggs together, in others they produce a capsule or other covering which protects the eggs.

The spermathecal gland.—In many insects there is a gland that opens either into the spermatheca or near the opening of the spermatheca, this is the *spermathecal gland* (Fig. 177, *sg*).

c. THE REPRODUCTIVE ORGANS OF THE MALE

The reproductive organs of the male are quite similar in their more general features to those of the female; but there are striking differences in details of form.

The general features of the testes.—As the reproductive elements developed in the testes, the spermatazoa, always remain small, the testes of a male are usually much smaller than the ovaries of the female of the same species.

In the more common form, each testis is a compact body (Fig. 181, *t*) composed of a variable number of tubes corresponding with the ovarian tubes, these are commonly called the *testicular follicles;* but it would have been better to have termed them the testicular tubes, reserving the term follicle for their divisions.

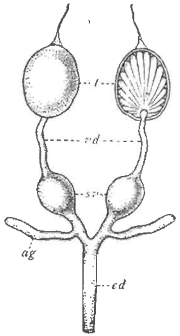

Fig. 181.—Diagram of the reproductive organs of a male insect; the right testis is shown in section; *ag*, accessory glands; *ed*, ejaculatory duct; *sv*, seminal vesicles; *t*, testes; *vd*, vasa deferentia.

The testicular follicles vary in number, form, and in their arrangement. In many insects as the Neuroptera, the Hemiptera, the Diptera, and in *Campodea* and *Japyx*, each testis is composed of a single follicle. In some beetles, Carabidæ and Elateridæ, the follicle is long and rolled into a ball. In some Thysanura the testicular follicles have a metameric arrangement.

In some Coleoptera, each testis is separated into several masses, each having its own outlet leading to the vas deferens; while in some other insects the two testes approach each other during the pupal stage and constitute in the adult a single mass.

The structure of a testicular follicle.—Like the ovarian tubes, the testicular follicles are lined with an epithelial layer, which is supported by a basement membrane, outside of which there is a peritoneal envelope composed of connective tissue. And in these follicles a series of zones are distinguished in which the genital cells are found in different stages of development, corresponding to the successive generations of these cells. In addition to the terminal filament four zones are recognized as follows:

The germarium.—This includes the primordial germ-cells and the spermatogonia.

The zone of growth.—Here are produced the spermatocytes of the first order and the spermatocytes of the second order.

The zone of division and reduction.—In this zone are produced the spermatids or immature spermatozoa.

The zone of transformation.—Here the spermatids become spermatozoa.

A discussion of the details of the development of the successive generations of the genital cells of the male, or spermatogenesis, does not fall within the scope of this volume.

The spermatophores.—In some insects the spermatozoa become enveloped in a sac in which they are transferred to the female; this sac is the *spermatophore*. Spermatophores have been observed in Gryllidæ, Locustidæ, and certain Lepidoptera.

Other structures.—A *ligament of the testis*, corresponding to the ligament of the ovary, is often present; the common outlet of the testicular follicles, corresponding to the oviduct is termed the *vas deferens* (Fig. 181, *vd*); an enlarged portion of the vas deferens serving as a reservoir for the products of the testis is known as a *seminal vesicle* (Fig. 181, *sv*); the invaginated portion of the body-wall, corresponding with the vagina of the female, is the *ejaculatory duct* (Fig. 181, *ed*); *accessory glands*, corresponding to the colleterial glands of the female, are present (Fig. 181, *ag*); the function of these glands has not been determined, they may secrete the fluid part of the semen, and they probably secrete the spermatophore when one is formed; *the penis*, this is merely the chitinized terminal portion of the ejaculatory duct, which can be evaginated with a part of the invaginated portion of the body-wall. It is furnished with powerful muscles for its protrusion and retraction.

XVI. THE SUSPENSORIA OF THE VISCERA

The organs discussed here do not constitute a well-defined system, but are isolated structures connected with different viscera. As in most cases they appear to serve a suspensory function, they are grouped together provisionally as the suspensoria of the viscera.

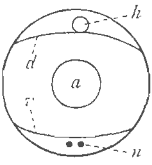

Fig. 182.—Diagram showing the relation of the dorsal diaphragm and the ventral diaphragm to other viscera: *a*, alimentary canal; *d*, dorsal diaphragm; *h*, heart; *n*, ventral nervous system; *v*, ventral diaphragm.

The dorsal diaphragm.—This is a membranous structure which extends across the abdominal cavity immediately below the heart, to which it is attached along its median line. The lateral margins of this diaphragm are attached to the sides of the body by a series of triangular prolongations, which have been commonly known as the *wings of the heart* (Fig. 139, *c*). The dorsal diaphragm is composed largely of very delicate muscles. Its relation to the heart is illustrated by the accompanying diagram (Fig. 182, *d*).

There are differences of opinion as to the function of the dorsal diaphragm. An important function is probably to protect the heart

from the peristaltic movements of the alimentary canal. It also supports the heart; and it may play a part in its expansion.

The dorsal diaphragm is also known as the *pericardial diaphragm*.

The ventral diaphragm.—The ventral diaphragm is a very delicate membrane which extends across the abdominal cavity immediately above the ganglia of the central nervous system. It is quite similar in form to the dorsal diaphragm; it is attached along each side of the body, just lateral of the great ventral muscles, by a series of prolongations resembling in form the wings of the heart. The position of the ventral diaphragm is illustrated in Figure 182, *v*.

This diaphragm has been described as a ventral heart; but I believe that its function is to protect the abdominal ganglia of the central nervous system from the peristaltic movements of the alimentary canal.

The thread-like suspensoria of the viscera.—Under this head may be classed the ligament of the ovary and the ligament of the testis, already described. In addition to these, there is, in some insects at least, a thread-like ligament that is attached to the intestine.

XVII. SUPPLEMENTARY DEFINITIONS

There are found in the bodies of insects certain organs not referred to in the foregoing general account of the internal anatomy of insects. These organs, though doubtless very important to the insects in which they occur, are not likely to be studied in an elementary course in entomology and, therefore, a detailed account of them may well be omitted from an introductory text-book. This is especially true as our knowledge of the structure and functions of these organs is so incomplete that an adequate discussion of the conflicting views now held would require more space than can be devoted to it here. The organs in question are the following:

The œnocytes.—The term *œnocytes* is applied to certain very large cells, that are found in clusters, often metamerically arranged, and connected with the tracheæ and the fat body of insects. The name was suggested by the light yellow color which often characterizes these cells, the color of certain wines; but the name is not a good one, as œnocytes vary greatly in color. Several other names have been applied to them but they are generally known by the name used here. Two types of œnocytes are recognized: first, the larval œnocytes; and second, the imaginal œnocytes.

The larval œnocytes are believed by Verson and Bisson ('91) to be ductless glands which take up, elaborate, and return to the blood definite substances, which may then be taken up by other cells of the body. Other views are held by other writers, but the view given above seems, as this time, to be the one best supported by the evidence at hand.

As to the function of the imaginal œnocytes, there are some observations that seem to show that they are excretory organs without ducts, cells that serve as storehouses for excretory products, becoming more filled with these products with the advancing age of the insect.

The pericardial cells.—The term *pericardial cells* is applied to a distinct type of cells that are found on either side of the heart in the pericardial sinus or crowded between the fibers of the pericardial diaphragm.

These cells can be rendered very conspicuous by injecting ammonia carmine into the living insect some time before killing and dissecting it; by this method the pericardial cells are stained deeply while the other cells of the body remain uncolored.

It is believed that the pericardial cells absorb albuminoids originating from the food and transform them into assimilable substances.

The phagocytic organs.—The term *phagocyte* is commonly applied to any leucocyte or white blood corpuscle that shows special activity in ingesting and digesting waste and harmful materials, as disintegrating tissue, bacteria, etc. The action of phagocytes is termed *phagocytosis;* an excellent example of phagocytosis is the part played by the leucocytes in the breaking down and rebuilding of tissues in the course of the metamorphosis of insects; this is discussed in the next chapter.

Phagocytosis may take place in any part of the body bathed by the blood and thus reached by leucocytes. In addition to this widely distributed phagocytosis, it is believed that in certain insects there are localized masses of cells which perform a similar function; these masses of cells are known as the *phagocytic organs.*

Phagocytic organs have been found in many Orthoptera and in earwigs; they are situated in the pericardial region; and can be made conspicuous by injecting a mixture of ammonia carmine and India ink into the body cavity; by this method the pericardial cells are stained red and the phagocytic organs black.

The light-organs.—The presence of organs for producing light is widely distributed among living forms both animal and vegetable.

The most commonly observed examples of light-producing insects are certain members of the Lampyridæ, the fireflies and the glow-worms, and a member of the Elateridæ, the "cucujo" of the tropics. With these insects the production of light is a normal function of highly specialized organs, the light-organs.

Examples of insects in which the production of light is occasionally observed are larvæ of mosquitoes, and certain lepidopterous larvæ. In these cases the production of light is abnormal, being due either to the presence in the body of light-producing bacteria or to the ingestion of luminescent food.

The position of the specialized light-organs of insects varies greatly; in the fireflies, they are situated on the ventral side of the abdomen; in the glow-worms, along the sides of the abdomen; and in the cucujo, the principal organs are in a pair of tubercles on the dorsal side of the prothorax and in a patch in the ventral region of the metathorax.

The structure of the light-organs of insects varies in different insects, as is shown by the investigations of several authors. A good example of highly specialized light-organs are those of *Photinus marginellus*, one of our common fireflies. An excellent account of these is that of Miss Townsend ('04), to which the reader is referred.

CHAPTER IV.

THE METAMORPHOSIS OF INSECTS

MANY insects in the course of their lives undergo remarkable changes in form; a butterfly was once a caterpillar, a bee lived first the life of a clumsy footless grub, and flies, which are so graceful and active, are developed from maggots.

In the following chapters considerable attention is given to descriptions of the changes through which various insects pass; the object of this chapter is merely to discuss the more general features of the metamorphosis of insects, and to define the terms commonly used in descriptions of insect transformations.

I. THE EXTERNAL CHARACTERISTICS OF THE METAMORPHOSIS OF INSECTS

The more obvious characteristics of the metamorphosis of insects are those changes in the external form of the body that occur during postembryonic development. In some cases there appears to be but little in common between the successive forms presented by the same insect, as the caterpillar, chrysalis, and adult stages of a butterfly. On the other hand, in certain insects, the change in the form of the body during the postembryonic life is comparatively little. Based on these differences, several distinct types of metamorphosis have been recognized; and in those cases where the insect in its successive stages assumes different forms, distinctive terms are applied to the different stages.

a. THE EGG

Strictly speaking, all insects are developed from eggs, which are formed from the primordial germ-cells in the ovary of the female. As a rule, each egg is surrounded by a shell, formed by the follicular epithelium of the ovarian tube in which the egg is developed; and this egg, enclosed in its shell, is deposited by the female insect, usually on or near the food upon which the young insect is to feed. In some cases, however, the egg is retained by the female until it is hatched; thus flesh-flies frequently deposit active larvæ upon meat, especially when they have had difficulty in finding it; and there are other viviparous insects, which are discussed later. In this place is discussed

the more common type of insect eggs, those that are laid while still enclosed in their shell.

The shape of the egg.—The terms ovoid and ovate have a definite meaning which has been derived from the shape of the eggs of birds; but while many eggs of insects are ovate in form, many others are not.

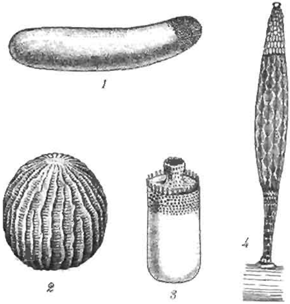

Fig. 183.—Eggs of insects: 1, *Œcanthus nigricornis;* 2, *Œnis semidea;* 3, *Piezosterum subulatum;* 4, *Hydrometra martini.*

The more common form of insect eggs is an elongate oval, somewhat curved; this type is illustrated by the eggs of crickets (Fig. 183, 1); many eggs are approximately spherical, as those of some butterflies (Fig 183, 2); while some are of remarkable shape, two of these are represented in Figure 183, 3, 4.

The sculpture of the shell.—Almost always the external surface of the shell of an insect egg is marked with small, hexagonal areas; these are the imprints of the cells of the follicular epithelium, which formed the shell. In many cases the ornamentation of the shell is very conspicuous, consisting of prominent ridges or series of tubercles; this is well-shown in the eggs of many Lepidoptera (Fig. 184).

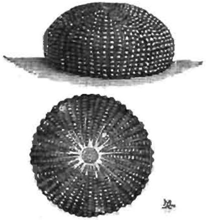

Fig. 184.—Egg of the cotton-worm moth; the micropyle is shown in the center of the lower figure.

The micropyle.—It has been shown, in the course of the discussion of the reproductive organs of the female, that the egg becomes full-grown, and the protecting chorion or egg-shell is formed about it before it is fertilized. This renders necessary some provision for the entrance of the male germ-cell into the egg; this provision consists of one or more openings in the shell through which a spermatozoan may enter. This opening or group of openings is termed the *micropyle*.

The number and position of the micropylar openings varies greatly in the eggs of different insects. Frequently they present an elaborate pattern at one pole of the egg (Fig. 184); and sometimes they open through more or less elongated papillæ (Fig. 185).

While in most cases it is necessary that an egg be fertilized in order that development may continue; there are many instances of parthenogenesis among insects.

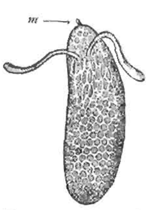
Fig. 185.—Egg of *Drosophila ampelophila*; *m*, micropyle.

The number of eggs produced by insects.—A very wide variation exists in the number of eggs produced by insects. In the sheep-tick, for example, a single large egg is produced at a time, and but few are produced during the life of the insect; on the other hand, in social insects, as ants, bees, and termites, a single queen may produce hundreds of thousands of eggs during her lifetime.

These, however, are extreme examples; the peculiar mode of development of the larva of the sheep-tick within the body of the female makes possible the production of but few eggs; while the division of labor in the colonies of social insects, by which the function of the queen is merely the production of eggs, makes it possible for her to produce an immense number; this is especially true where the egg-laying period of the queen extends over several years.

The following may be taken as less extreme examples. In the solitary nest-building insects, as the fossores, the solitary wasps, and the solitary bees, the great labor involved in making and provisioning the nest results in the reduction of the number of eggs produced to a comparatively small number; while many insects that make no provision for their young, as moths, for example, may lay several hundred eggs.

With certain chalcis-flies the number of young produced is not dependent upon the number of eggs laid; for with these insects many embryos are developed from a single egg. This type of development is termed *polyembryony*.

Modes of laying eggs.—Perhaps in no respect are the wonderful instincts of insects exhibited in a more remarkable way than in the manner of laying their eggs. If insects were reasoning beings, and if each female knew the needs of her young to be, she could not more accurately make provision for them than is now done by the great majority of insects.

This is especially striking where the life of the young is entirely different from that of the adult. The butterfly or moth may sip nectar from any flower; but when the female lays her eggs, she selects with unerring accuracy the particular kind of plant upon which her larvæ feed. The dragonfly which hunts its prey over the field, returns to water and lays her eggs in such a position that the young when it leaves the egg is either in or can readily find the element in which alone it is fitted to live.

The ichneumon-flies frequent flowers; but when the time comes for a female to lay her eggs, she seeks the particular kind of larva upon which the species is parasitic, and will lay her eggs in no other. It is a remarkable fact that no larva leads so secluded a life that it cannot be found by its parasites. Thus the larvæ of *Tremex Columba* bore in solid wood, where they are out of sight and protected by a layer of wood and the bark of the tree in which they are boring; nevertheless the ichneumon-fly *Thalessa lunator*, which is parasitic upon it, places her eggs in the burrows of the *Tremex* by means of her long drill-like ovipositor (Fig. 186).

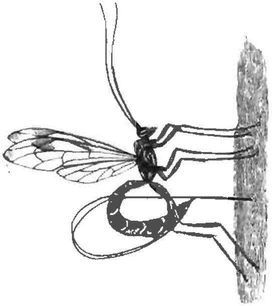

Fig. 186.—*Thalessa lunator.*

In contrast with the examples just cited, some insects exhibit no remarkable instinct in their egg-laying. Our common northern walking-stick, *Diapheromera*, drops its eggs on the ground under the shrubs and trees upon which it feeds. This, however, is sufficient provision, for the eggs are protected throughout the winter by the fallen leaves, and the young when hatched, readily find their food.

Many species, the young of which feed upon foliage lay their eggs singly upon leaves; but many others, and this is especially true of those, the young of which are gregarious, lay their eggs in clusters. In some cases, as in the squash bug, the mass of eggs is not protected (Fig. 187); in others, where the duration of the egg-state is long, the eggs are protected by some covering. The females of our tent-caterpillars cover their eggs with a water-proof coating; and the tussock moths of the genus *Hemerocampa* cover their egg-clusters with a frothy mass.

The laying of eggs in compact masses, however, is not correlated, in most cases, with gregarious habits of the larvæ. The water-scavenger beetles, Hydrophilidæ, make egg-sacks out of a hardened silk-like secretion (Fig. 188); the locusts, Acridiidæ, lay their eggs in oval masses and cover them with a tough substance; the scale-insects of the genus *Pulvinaria* excrete a large cottony egg-sac (Fig. 189);

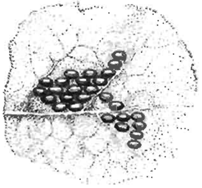

Fig. 187.—Egg-mass of the squash-bug.

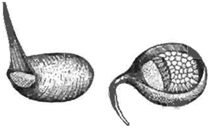

Fig. 188.—Egg-sac of *Hydrophilus* (After Miall).

the eggs of the praying mantis are laid in masses and overlaid with a hard covering of silk (Fig. 190); and cockroaches produce pod-like egg-cases, termed ootheca, each containing many eggs (Fig. 191).

Fig. 190.—Egg-mass of a praying mantis.

Fig. 189.—*Pulvinaria innumerabilis*, females on grape with egg-sacs.

Among the more remarkable of the methods of caring for eggs is that of the lace-winged flies, *Chrysopa*. These insects place each of their eggs on the summit of a stiff stalk of hard silk (Fig. 192).

Duration of the egg-state.—In the life-cycle of most insects, a few days, and only a few, intervene between the laying of an egg and the emergence of the nymph, naiad, or larva from it. In some the duration of the egg-state is even shorter, the hatching of the egg taking place very soon after it is laid, or even, as sometimes in flesh-flies, before it is laid. On the other hand, in certain species, the greater part of the life of an individual is passed within the egg-shell. The common apple-tree tent-caterpillars, *Clisiocampa americana*, lays its eggs in early summer; but these eggs do not hatch till the following spring; while the remainder of the life-cycle occupies only a

few weeks. The eggs of *Bittacus* are said to remain unhatched for two years; and a similar statement is made regarding the eggs of our common walking-stick.

b. THE HATCHING OF YOUNG INSECTS

Fig. 191.—Ootheca of a cockroach.

Only a few accounts have been published regarding the manner in which a young insect frees itself from the embryonic envelopes. In some cases it is evident that the larva cuts its way out from the egg-shell by means of its mandibles; but in others, a specialized organ has been developed for this purpose.

Fig. 192.—Eggs, larva, cocoon, and adult of *Chrysopa*.

The hatching spines.—An organ for rupturing the embryonic envelopes is probably commonly present. It has been described under several names. It was termed an *egg-burster* by Hagen, the *ruptor ovi* by C. V. Riley an *egg-tooth* by Heymons, and the *hatching spines* by Wheeler.

c. THE MOLTING OF INSECTS

The young of insects cast periodically the outer parts of the cuticula; this process is termed *molting* or *ecdysis*.

General features of the molting of insects.—The chitinization of the epidermis or primary cuticula adds to its efficiency as an armor, but it prevents the expansion of the body-wall rendered necessary by the growth of the insect; consequently as the body grows, its cuticula becomes too small for it. When this occurs a second epidermis is formed by the hypodermis; after which the old epidermis splits open, usually along the back of the head and thorax, and the insect works itself out from it. The new epidermis being elastic, accommodates itself to the increased size of the body; but in a short time it becomes chitinized; and as the insect grows it in turn is cast off. The cast skin of an insect is termed the *exuviæ*, the plural noun being used as in English is the word clothes.

Coincident with the formation of the new epidermis, new setæ are formed beneath the old epidermis; these lie closely oppressed to the outer surface of the new epidermis until released by the molting of the old epidermis.

In the above account only the more general features of the process of molting are indicated, the details, according to the observations of Tower ('06) are as follows. (See Figure 113, p. 99). In the formation of the new epidermis it appears as a thin, delicate lamella, spread evenly over the entire outer surface of the hypodermis; it grows rapidly in thickness until finally, just before ecdysis takes place, it reaches its final thickness. After ecdysis the epidermis hardens rapidly and its coloration is developed. As soon as ecdysis is over the deposition of the dermis or secondary cuticula begins. This layer is a carbohydrate related to cellulose, and is deposited in layers of alternating composition, through the period of reconstruction and growth, during which it reaches its maximum thickness. Preliminary to ecdysis a thin layer of molting fluid is formed, and through its action the old dermis is corroded and often almost entirely destroyed, thus facilitating ecdysis. This dissolving of the dermis, is, according to Tower, a most constant phenomenon in ecydsis; and has been found in all insects examined by him in varying degrees.

It is said that the Collembola molt after reaching sexual maturity, in this respect agreeing with the Crustacea and the "Myriapoda," and differing from the Arachnida and from all other insects (Brindley '98).

The molting fluid.—As indicated above, the process of molting is facilitated by the excretion of a fluid known as the molting fluid. This is produced by unicellular glands (Fig. 113, p. 99) which are modified hypodermal cells. These glands are found all through the life of the insect and upon all parts of the body; but are most abundant upon the pronotum, and are more abundant at pupation than at any other period.

The number of postembryonic molts.—A very wide range of variation exists as to number of molts undergone by insects after they leave the egg-shell. According to Grassi ('98, p. 292), there is only a single partial molt with *Campodea* and *Japyx*, while the May-fly *Chloeon* molts twenty times. Between these extremes every condition exists. Probably the majority of insects molt from four to six times; but there are many records of insects that molt many more times than this.

Stadia.—The intervals between the ecdyses are called *stadia*. In numbering the stadia, the first stadium is the period between hatching and the first postembryonic ecdysis.

Instars.—The term *instar* is applied to the form of an insect during a stadium; in numbering the instars, the form assumed by the insect between hatching and the first postembryonic molt is termed the first instar.

Head measurements of larvæ.—It was demonstrated by Dyar ('90) that the widths of the head of a larva in its successive instars follow a regular geometric progression in their increase. The head was selected as a part not subject to growth during a stadium; and the width as the most convenient measurement to take. By means of this criterion, it is possible to determine, when studying the transformations of an insect, whether an ecdysis has been overlooked or not. Experience has shown that slight variations between the computed and the actual widths may occur; but these differences are so slight that the overlooking of an ecdysis can be readily discovered. The following example will serve to illustrate the method employed.

A larva of *Papilio thoas* was reared from the egg; and the widths of the head in the successive instars was found to be, expressed in millimeters, as follows: .6; 1.1; 1.6; 2.2; 3.4.

By dividing 2.2. by 3.4 (two successive members of this series), the ratio of increase was found to be .676+; the number, .68 was taken, therefore, as sufficiently near the ratio for practical purposes. By using this ratio as a factor the following results were obtained:

Width found in fifth instar			. . . .	3.4
Calculated width in fourth instar			($3.4 \times .68$) = ...	2.312
" " "	third	"	($2.312 \times .68$) = .	1.57
" " "	second	"	($1.57 \times .68$) = . .	1.067
" " "	first		($1.067 \times .68$) = . . .	.725

By comparing the two series, as is done below, so close a correspondence is found that it is evident that no ecdysis was overlooked.

Widths found:—.6; 1.1; 1.6; 2.2; 3.4

" calculated:—.7; 1.1–; 1.6–; 2.3.

Fig. 193.—A spider in which lost legs were being reproduced.

The reproduction of lost limbs.—The reproduction of lost limbs has been observed in many insects; but such reproduction occurs here much less frequently than in the other classes of the Arthropoda. The reproduction takes place during the period of ecdysis, the reproduced part becoming larger and larger with each molt; hence with insects, and with Arachnida as well, the power of reproducing lost limbs ceases with the attainment of sexual maturity; but not so with the Crustacea and the "Myriapoda" which molt after becoming sexually mature. In none of the observed examples of the reproduction of appendages has an entire leg been reproduced.

It appears to be necessary that the original coxa be not removed in order that the reproduction may take place. Figure 193 represents a spider in our collection in which two legs, the left fore leg and the right hind leg, were being reproduced when the specimen was captured.

d. DEVELOPMENT WITHOUT METAMORPHOSIS
(*Ametabolous** *Development*)

While most insects undergo remarkable changes in form during their postembryonic development, there are some in which this is not the case. In these the young insect just hatched from the egg is of practically the same form as the adult insect. These insects grow larger and may undergo slight changes in form of the body and its appendages; but these changes are not sufficiently marked to merit being termed a metamorphosis. This type of development is known technically as *ametăbolous development.*

Development without metamorphosis is characteristic of the two orders Thysanura and Collembola, which in other respects, also, are the most generalized of insects.

The nature of the changes in form undergone by an insect with an ametabolous development is illustrated by the development of *Machilis alternata*, one of the Thysanura. The first instar of this insect, according to Heymons ('07), lacks the clothing of scales, the styli on the thoracic legs, and the lateral rows of eversible sacs on the abdominal segments; and the antennæ and cerci are relatively shorter and consist of a much smaller number of segments than those of the adult. These changes, however, are comparable with those undergone by many animals in the course of their development that are not regarded as having a metamorphosis. In common usage in works on Entomology the term metamorphosis is used to indicate those marked changes that take place in the appearance of an insect that are correlated with the development of wings.

In addition to the Thysanura and the Collembola there are certain insects that develop without metmorphosis, as the Mallophaga and the Pediculidæ. But their ametabolous condition is believed to be an acquired one. In other words, it is believed that the bird-lice and the true lice are descendants of winged insects whose form of body and mode of development have been modified as a result of parasitic life.

The Ametabola.—Those insects that develop without metamorphosis are sometimes referred to as the *Ametabola*. This term was first proposed by Leach (1815), who included under it the lice as well as the Thysanura and Collembola. But with our present knowledge, if it is used it should be restricted to the Thysanura and Collembola; those insects in which a development without metamorphosis is a primitive not an acquired condition.

*Ametăbolous: Greek *a*, without; *metabole* (μεταβολή), change.

e. GRADUAL METAMORPHOSIS

(*Paurometabolous* Development*)

In several orders of insects there exists a type of development that is characterized by the fact that the young resemble the adult in the general form of the body and in manner of life. There is a gradual growth of the body and of the wing rudiments and genital appendages.

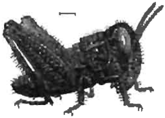

Fig. 194.—Nymph of *Melanoplus*, first instar (After Emerton)

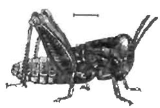

Fig. 195.—Nymph of *Melanoplus*, second instar (After Emerton).

Fig. 196.—Nymph of *Melanoplus*, third instar (After Emerton)

Fig. 197.—Nymph of *Melanoplus*, fourth instar (After Emerton).

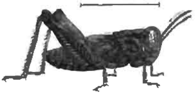

Fig. 198.—Nymph of *Melanoplus*, fifth instar (After Emerton).

Fig. 199.—*Melanoplus*, adult.

But the changes in form take place gradually and are not very great between any two successive instars except that at the last ecdysis there takes place a greater change, especially in the wings, than at any of the preceding ecdyses. This type of metamorphosis is designated as *gradual metamorphosis* or *paurometabolous development*.

The characteristic features of paurometabolous development are correlated with the fact that the mode of life of the young and of the

*Paurometăbolous: *pauros* (παῦρος), little; *metabole* (μεταβολή), change.

adult are essentially the same; the two living in the same situation, and feeding on the same food. The adult has increased power of locomotion, due to the completion of the development of the wings; this enables it to more readily perform the functions of the adult, the spread of the species, and the making of provision for its continuance; but *otherwise the life of the adult is very similar to that of the young.*

The development of a locust or short-horned grasshopper will serve as an example of gradual metamorphosis. Each of the instars of our common red-legged locust, *Melanoplus femur-rubrum*, is represented in the accompanying series of figures. The adult (Fig. 199) is represented natural size; each of the other instars, somewhat enlarged; the hair line above the figure in each case indicates the length of the insect.

The young locust just out from the egg-shell can be easily recognized as a locust (Fig. 194). It is of course much smaller than the adult; the proportion of the different regions of the body are somewhat different; and it is not furnished with wings; still the form of the body is essentially the same as that of the adult. In the second and third instars (Fig. 195 and 196) there are slight indications of the development of wing-rudiments; and these rudimentary wings are quite conspicuous in the fourth and fifth instars (Fig. 197 and 198). The change at the last ecdysis, that from the fifth instar to the adult, is more striking than that at any preceding ecdysis; this is due to the complete expansion of the wings, which takes place at this time.

The Paurometabola.—Those orders of insects that are characterized by a gradual metamorphosis are grouped together as the *Paurometabola*. This is not a natural division of the class Hexapoda but merely indicates a similarity in the nature of the metamorphosis in the orders included. This group includes the Isoptera, Dermaptera, Orthoptera, Corrodentia, Thysanoptera, Homoptera, and Heteroptera.

The term nymph.—An immature instar of an insect that undergoes a gradual metamorphosis is termed a *nymph*.

In old entomological works, and especially in those written in the early part of the last century, the term nymph was used as a synonym of pupa; but in more recent works it is applied to the immature instar of insects that undergo either a gradual or incomplete metamorphosis In this book I restrict the use of this term to designate an immature instar of an insect that undergoes a gradual metamorphosis.

Deviation from the usual type.—It is to be expected that within so large a group of organisms as the Paurometabola there should have

been evolved forms that exhibit deviations from the usual type of development. The more familiar examples of these are the following:

The Saltitorial Orthoptera.—In the crickets, locusts, and long-horned grasshoppers, the wings of the nymphs are developed in an inverted position; that surface of the wing which is on the outside in the adult is next to the body in the nymphal instars; and the rudimentary hind wings are outside of the fore wings, instead of beneath them, as in the adult. At the last ecdysis the wings assume the normal position.

The Cicadas.—In the Cicadas there exists a greater difference between the nymphal instars and the adult than is usual with insects in which the metamorphosis is gradual. The nymphs live below the surface of the ground, feeding upon the roots of plants; the adults live in the open air, chiefly among the branches of trees. The forelegs of the nymphs are fossorial (Fig. 200); this is an adaptation for subterranean life, which is not needed and not possessed by the adults. And it is said that the last nymphal instar is quiescent for a period.

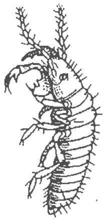

Fig. 200.—Nymph of a *Cicada* (After Riley).

The Coccidæ.—In the Coccidæ the mode of development of the two sexes differ greatly. The female never acquires wings, and in so far as external form is concerned the adult is degenerate. The male, on the other hand, exhibits a striking approach to complete metamorphosis, the last nymphal instar being enclosed in a cocoon, and the legs of the adult are not those of the nymph, being developed from imaginal disks. But the wings are developed externally.

The Aleyrodidæ.—In this family the type of metamorphosis corresponds quite closely with that described later as complete metamorphosis; consequently the term larva is applied to the immature instars except the last, which is designated the pupa.

The wings arise as histoblasts in the late embryo, and the growth of the wing-buds during the larval stadia takes place inside the body-wall. The change to the pupal instar, in which the wing-buds are external, takes place beneath the last larval skin, which is known as the pupa case or puparium. The adult emerges through a T-shaped opening on the dorsum of the puparium. Both sexes are winged.

The Aphididæ.—In the Aphididæ there exists a remarkable type of development known as ***hĕterŏgamy*** or cyclic reproduction. This is characterized by an alternation of several parthenogenetic generations

with a sexual generation. And within the series of parthenogenetic forms there may be an alternation of winged and wingless forms. In some cases the reproductive cycle is an exceedingly complicated one; and different parts of it occur on different food plants.

The Thysanoptera.—In the Thysanoptera, as in most other insects with a gradual metamorphosis, the nymphs resemble the adults in the form of the body, and the wings are developed externally; but the last nymphal instar is quiescent or nearly so and takes no nourishment. This instar is commonly described as the pupa.

f. INCOMPLETE METAMORPHOSIS

(*Hemimetabolous* Development*)

In three of the orders of insects, the Plecoptera, Ephemerida, and Odonata, there exists a type of metamorphosis in which the changes

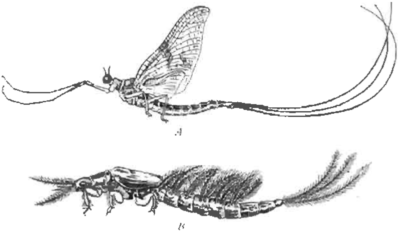

Fig. 201.—Transformation of a May-fly, *Ephemera varia;* A, adult; B, naiad (After Needham).

that take place in the form of the body are greater than in gradual metamorphosis but much less marked than in complete metamorphosis. For this reason the terms *incomplete metamorphosis* and *hemimetabolous development* have been applied to it.

Both incomplete metamorphosis and complete metamorphosis are characterized by the fact that the immature instars exhibit adaptive modifications of form and structure, fitting them for a very different mode of life than that followed by the adult. This is often expressed by the statement that the immature instars are "sidewise developed"; for it is believed that in these cases the development of the individual does not repeat the history of the race to which the individual belongs.

*Hemimetăbolous: *hemi* (ἡμί), half; *metabŏle* (μεταβολή), change.

This mode of development is termed *cenogenisis*.* It contrasts strongly with gradual metamorphosis, where there is a direct development from the egg to the adult.

In each of the orders that are characterized by an incomplete metamorphosis, the adaptive characteristics of the young insects fit them for aquatic life; while the adults lead an aerial existence. The transformations of a May-fly (Fig. 201) will serve to illustrate this type of metamorphosis.

The primitive insects were doubtless terrestrial; this is shown by the nature of the respiratory system, which is aerial in all insects. In the course of the evolution of the different orders of insects, the immature forms of some of them invaded the water in search of food. This resulted in a sidewise development of these immature forms to better fit them to live in this medium; while the adult continued their development in, what may be termed by contrast, a direct line. In some of the Plecoptera, as *Capnia* and others, the results of the cenogenetic development are not marked except that the immature forms are aquatic.

In the three orders in which the metamorphosis is incomplete, the cenogenetic development of the immature instars involved neither a change in the manner of development of the wings nor a retarding of the development of the compound eyes; consequently these immature forms, although sidewise developed, constitute a class quite distinct from larvæ.

The Hemimetabola.—The three orders in which the development is a hemimetabolous one are grouped together as the *Hemimetăbola;* these are the Plecoptera, Ephemerida, and Odonata. This grouping together of these three orders is merely for convenience in discussions of types of metamorphosis and does not indicate a natural division of the class Hexapoda. The radical differences in the three types of aquatic respiratory organs characteristic of the three orders indicate that they were evolved independently.

The term naiad.—The immature instars of insects with an incomplete metamorphosis have been termed nymphs; but as a result of their sidewise development they do not properly belong in the same class as the immature instars of insects with a gradual metamorphosis. I, therefore, proposed to designate them as *naiads* (Comstock '18, *b*).

The adoption of the term naiad in this sense affords a distinctive term for each of the three classes of immature insects corresponding to the three types of metamorphosis, *i. e.*, nymphs, naiads, and larvæ.

*Cēnogĕnisis: *kainos* (καινος), new; *genesis*.

Deviation from the usual type of incomplete metamorphosis.—The more striking deviations from the usual type of hemimetabolous development are the following:

The Odonata.—In the Odonata the wings of the naiads are inverted; these insects resembling in this respect the Saltitorial Orthoptera. What is the upper surface of the wings with naiads becomes the lower surface in the adults, the change taking place at the last ecdysis.

The Ephemerida.—In the Ephemerida, there exists the remarkable phenomenon of an ecdysis taking place after the insect has left the water and acquired functional wings. The winged instar that is interpolated between the last aquatic one and the adult is termed the *sub-imago.*

g. COMPLETE METAMORPHOSIS

(*Holometabolus* Development*)

The representatives of several orders of insects leave the egg-shell in an entirely different form from that they assume when they reach maturity; familiar examples of these are caterpillars which develop into butterflies, maggots which develop into flies, and grubs which develop into beetles. These insects and others that when they emerge from the egg-shell bear almost no resemblance in form to the adult are said to undergo a *complete metamorphosis* or a *holometăbolous development.*

The Holometabola.—Those orders that are characterized by a holometabolous development are grouped together as the *Holometăb-ola.* This group includes the Neuroptera, Mecoptera, Trichoptera, Lepidoptera, Diptera, Siphonaptera, Coleoptera, and Hymenoptera.

This grouping together of these orders, while convenient for discussions of metamorphosis, is doubtless artificial. It is not at all probable that the Holometabola is a monophylitic group. In other words complete metamorphosis doubtless arose several times independently in the evolution of insects.

The term larva.—The form in which a holometabolous insect leaves the egg is called *larva.* The term was suggested by a belief of the ancients that the form of the perfect insect was masked, the Latin word *larva* meaning a mask.

Formerly the term larva was applied to the immature stages of all insects; but more recent writers restrict its use to the immature in-

*Holometăbolous: *holos* (ὅλος), complete; *metabole* (μεταβολή), change.

stars of insects with a complete metamorphosis; and in this sense only is it used in this book.

The adaptive characteristics of larvæ.—The larvæ of insects with complete metamorphosis, like the naiads of those with incomplete metamorphosis, exhibit an acquired form of body adapting them to special modes of life; and in this case the cenogenetic or "sidewise development" is much more marked than it is in insects with an incomplete metamorphosis. Here the form of the body bears but little relation to the form to be assumed by the adult, the nature of the larval life being the controlling factor.

The differences in form between larvæ and adults are augmented by the fact that not only have larvæ been modified for special modes of life, but in most cases the adults have been highly specialized for a different mode of life; and so great are these differences that a quiescent pupa stage, during which certain parts of the body can be made over, is necessary.

Here, as in the case of insects with an incomplete metamorphosis, we have an illustration of the fact that natural selection can act on any stage in the development of animal to better adapt that particular stage to the conditions under which it exists. Darwin pointed out in his "Origin of Species" that at whatever age a variation first appears in the parent it tends to reappear at a corresponding age in the offspring. This tendency is termed *homochronous heredity**.

It is obvious that the greater the adaptive characteristics of the immature forms, the less does the ontogeny of a species represent the phylogeny of the race to which it belongs. This fact led Fritz Muller, in his "Facts for Darwin", to make the aphorism "There were perfect insects before larvæ and pupæ." The overlooking of this principle frequently results in the drawing of unwarranted conclusions, by those writers on insects who cite adaptive larval characteristics as being more generalized than the corresponding features of the adult.

The more obvious of the adaptive characteristics of larvæ are the following:

The form of the body.—As indicated above the form of the body of a larva bears but little relation to the form to be assumed by the adult, the nature of the larval life being the controlling factor in determining the form of the body. As different larvæ live under widely differing situations, various types of larvæ have been developed; the more important of these types are described later.

The greater or less reduction of the thoracic legs.—In the evolution of most larvæ there has taken place a greater or less reduction of the thoracic legs; but the extent of this reduction varies greatly. The larvæ of certain Neuroptera, as *Corydalus* for example, have as perfect

*Homŏchronous: *homos* (ὁμός), one and the same; *chronos* (χρόνος), time.

legs as do naiads of insects with an incomplete matamorphosis. The larvæ of Lepidoptera have short legs which correspond to only a part of the legs of the adult. While the larvæ of Diptera have no external indications of legs.

The development of prolegs in some larvæ.—A striking feature of many larvæ is the presence of abdominal organs of locomotion; these have been termed *prolegs;* the prolegs of caterpillars are the most familiar examples of these organs.

The prolegs were so named because they were believed to be merely adaptive cuticular formations and not true legs; this belief arose from the fact that they are shed with the last larval skin. Some recent writers, however, regard the prolegs as true legs. It is now known that abdominal appendages are common in the embryos of insects; and these writers believe that the prolegs are developed from these embryonic appendages, and that, therefore, they must be regarded as true legs.

If this is true, there has taken place a remarkable reversal in the course of development. The abdominal legs, except those that were modified into appendages of the reproductive organs, the gonapophyses, were lost early in the phylogeny of the Hexapoda. The origin of complete metamorphosis must have taken place at a much later period; when, according to this belief, the abdominal appendages, which had been latent for a long time, were redeveloped into functional organs.

The development of tracheal gills.—A striking feature of many larvæ is the possession of tracheal gills. This is obviously an adaptive characteristic the development of which was correlated with the assumption of aquatic life by forms that were primarily aerial; and it is also obvious that the development of tracheal gills has arisen independently many times; for they exist in widely separated families belonging to different orders of insects that are chiefly aerial. They are possessed by a few lepidopterous larvæ, and by the representatives of several families of Neuroptera, Coleoptera and Diptera. On the other hand, in the Trichoptera the possession of tracheal gills by the larvæ is characteristic of nearly all members of the order.

The internal development of wings.—This is perhaps the most remarkable of the sidewise developments of larvæ. Although larvæ exhibit no external indications of wings, it has been found that the rudiments of these organs arise at as early a period in insects with a complete metamorphosis as they do in those with an incomplete metamorphosis; and that during larval life the wing rudiments attain an advanced stage in their development. But as these rudiments are invaginated there are no external indications of their presence during larval life. The details of the internal development of wings are discussed later.

Occasionally atavistic individual larvæ are found which have external wing-buds.

As to the causes that brought about the internal development of wings we can only make conjectures. It has occurred to the writer that this type of wing-development may have arisen as a result of boring habits, or habits of an analogous nature, of the stem forms from which the orders of the Holometabola sprang. Projecting wing-buds would interfere with the progress of a boring insect; and, therefore, an embedding of them in the body, thus leaving a smooth contour, would be advantageous.

In support of this theory attention may be called to the fact that the larvæ of the most generalized Lepidoptera, the Hepialidæ, are borers; the larvæ of the Siricidæ, which are among the more generalized of the Hymenoptera are borers; so too are many Coleoptera; most larvæ of Diptera are burrowers; and the larvæ of Trichoptera live in cases.

The retarding of the development of the compound eyes.—One of the most distinctively characteristic features of larvæ is the absence of compound eyes. The life of most larvæ is such that only limited vision is necessary for them; and correlated with this fact is a retarding of the development of the greater portion of the compound eyes; only a few separate ommatidia being functional during larval life.

In striking contrast with this condition are the well-developed eyes of nymphs and naiads.

The larvæ of *Corethra* are the only larvæ known to me that possess compound eyes.

The invaginated conditions of the head in the larvæ of the more specialized Diptera.—The extreme of sidewise development is exhibited by the larvæ of the more specialized Diptera. Here not only are the legs and wings developed internally but also the head. This phenomenon is discussed later.

The different types of larvæ.—As a rule, the larvæ of the insects of any order resemble each other in their more general characteristics, although they bear but little resemblance to the adult forms. Thus the grubs of Coleoptera, the caterpillars of Lepidoptera, or the maggots of Diptera, in most cases, can be recognized as such. Still in each of these orders there are larvæ that bear almost no resemblance to the usual type. As examples of these may be cited the water-pennies (Parnidæ, Coleoptera), the slug-caterpillars (Cochlidiidæ, Lepidoptera), and the larvæ of *Microdon* (Diptera).

To understand the variations in form of larvæ it should be borne in mind that the form of the body in all larvæ is the result of secondary adaptations to peculiar modes of life; and that this modification of form has proceeded in different directions and in varying degrees in different insects.

Among the many types of larvæ, there are a few that are of such common occurrence as to merit distinctive names; the more important of these are the following:

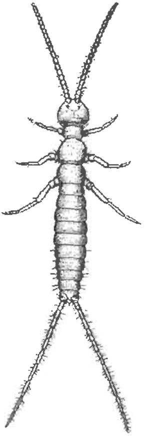

Fig. 202.—*Campodea staphylinus* (After Lubbock).

Campodeiform.—In many paurometabolous insects and in some holometabolous ones, the early instars resemble *Campodea* more or less in the form of the body (Fig. 202); such naiads and larvæ are described as *campodeiform.*

In this type, the body is long, more or less flattened, and with or without caudal setæ; the mandibles are well developed; and the legs are not greatly reduced. Among the examples of this type are the larvæ of most Neuroptera, and the active larvæ of many Coleoptera (Carabidæ, Dysticidæ, and the first instar of Meloidæ).

Eruciform.—The *eruciform* type of larvæ is well-illustrated by most larvæ of Lepidoptera and of Mecoptera; it is the caterpillar form (Fig. 203). In this type the body is cylindrical; the thoracic legs are short, having only the terminal portions of them developed; and the abdomen is furnished with prolegs or with proleg-like cuticular folds. Although these larvæ move freely, their powers of locomotion are much less than in the campodeiform type.

Scarabeiform.—The common white grub, the larva of the May-beetle (Fig. 204) is the most familiar example of a *scarabeiform* larva.

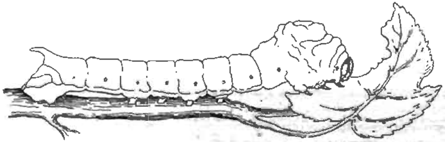

Fig. 203.—The silk-worm, an eruciform larva (After Verson).

In this type the body is nearly cylindrical, but usually, especially when at rest, its longitudinal axis is curved; the legs are short; and

prolegs are wanting. This type is quite characteristic of the larvæ of the Scarabæidæ, hence the name; but it occurs in other groups of insects.

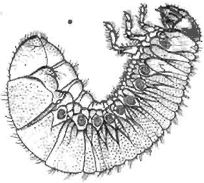

Fig. 204.—Larva of *Melolontha vulgaris* (After Schiodte).

The movements of these larvæ are slow; most of them live in the ground, or in wood, or in decaying animal or vegetable matter.

Vermiform.—Those larvæ that are more or less worm-like in form are termed *vermiform*. The most striking features of this type are the elongated form of the body and an absence of locomotive appendages (Fig. 205).

Naupliiform.—The term *naupliiform* is applied to the first instar of the larva of *Platygaster* (Fig. 206), on account of its resemblance to the nauplius of certain Crustacea.

Fig. 205.—Larva of a crane-fly.

The prepupa.—Usually the existence of an instar between the last larval one and the pupal instar is not recognized. But such a form exists; and the recognition of it becomes important when a careful study is made of the development of holometabolous insects. As is shown later, during larval life the development of the wings is going on within the body. As the larva approaches maturity, the wings reach an advanced stage of development within sac-like invaginations of the body-wall. Near the close of the last larval stadium the insect makes preparation for the change to the pupa state. Some form a cell within which the pupa state is passed, the larvæ of butterflies suspend themselves, and most larvæ of moths spin a cocoon. Then follows a period of apparent rest before the last larval skin is shed and the pupal state assumed. But this period is far from being a quiet one; within the apparently motionless body important changes take place. The most easily observed of these changes is a change in the position of the wings. Each of these passes out through the mouth of the sac in which it has been developed, and lies outside of the newly developed pupal cuticula, but beneath the last larval cuticula. Then follows a period of variable duration in different insects, in which the wings are really

outside of the body although still covered by the last larval cuticula; this period is the *prepupal* stadium. The prepupal instar differs markedly from both the last larval one and from the pupa; for after the shedding of the last larval cuticula important changes in the form of the body take place before the pupal instar is assumed

Fig. 206.—Larva of Platygaster (After Ganin.)

The pupa.—The most obvious characteristics of the pupa state are, except in a few cases, inactivity and helplessness. The organs of locomotion are functionless, and may even be soldered to the body throughout their entire length, as is usual with the pupæ of Lepidoptera (Fig. 207). In other cases, as in the Coleoptera (Fig. 208) and in the Hymenoptera, the wings and legs are free, but enclosed in more or less sac-like cuticular sheaths, which put them in the condition of the proverbial cat in gloves. More than this, in most cases, the legs of the adult are not fully formed till near the end of the pupal stadium.

The term *pupa*, meaning girl, was applied to this instar by Linnæus on account of its resemblance to a baby that has been swathed or bound up, as is the custom with many peoples.

Fig. 207.—Pupa of a moth.

Although the insect during the pupal stadium is apparently at rest, this, from a physiological point of view, is the most active period of its postembryonic existence: for wonderful changes in the structure of the body take place at this time.

In the development of a larva the primitive form of the body has been greatly modified to adapt it to its peculiar mode of life; this sidewise development results in the production of a type of body that is not at all fitted for the duties of adult life. In the case of an insect with incomplete metamorphosis, the full grown naiad needs to be modified comparatively little to fit it for adult life; but the change from a maggot to a fly, or from a caterpiller to a butterfly, involves not merely a change in external form but a greater or less remodeling of its entire structure. These changes take place during the period of apparent rest, the prepupal and pupal stadia.

Fig. 208 Pupa of a beetle.

The chrysalis.—The term *chrysalis* is often applied to the pupæ of butterflies. It was suggested by the golden spots with which the pupæ of certain butterflies are ornamented.

Two forms of this word are in use: first, chrysalis, the plural of which is chrysalides; and second, chrysalid, the plural of which is

chrysalids. The singular of the first form and the plural of the second are those most often used.

Active pupæ.—The pupæ of mosquitoes and of certain midges are remarkable for being active. Although the wings and legs are functionless, as with other pupæ, these creatures are able to swim by means of movements of the caudal end of the body.

In several genera of the Neuroptera (*Chrysopa*, *Hemerobius*, and *Raphidia*) the pupa becomes active and crawls about just before transforming to the adult state.

Movements of a less striking character are made by many pupæ, which work their way out of the ground, or from burrows in wood, before transforming. In some cases, as in the pupæ of the carpenter-moths (Cossidæ) the pupa is armed with rows of backward projecting teeth on the abdominal segments, which facilitate the movements within the burrow.

The cremaster.—Many pupæ, and especially those of most Lepidoptera, are provided with a variously shaped process of the posterior end of the body, to which the term *cremaster* is applied. This process is often provided with hooks which serve to suspend the pupa, as in butterflies, or to hold it in place, after it has partly emerged from the cocoon, and while the adult is emerging from the pupal skin, as in cocoon-making moths. In its more simple form, where hooks are lacking, it aids the pupa in working its way out of the earth, or from other closed situations.

The method of fixing the cremaster in the disk of silk from which the pupa of a butterfly is suspended was well-illustrated by C. V. Riley ('79). The full grown larva spins this disk and hangs from it during the prepupal stadium by means of its anal prolegs (Fig. 209, *a*). When the last larval skin is shed, it is worked back to the caudal end of the body (Fig. 209, *b*); and is then grasped between two of the abdominal segments (Fig. 209, *c*.) while the caudal end of the body is removed from it; and thus the cremaster is freed, and is in a position from which it can be inserted in the disk of silk.

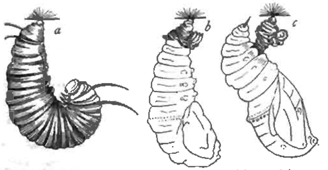

Fig. 209.—Transformations of the milkweed butterfly (From Riley).

The cocoon.—The pupal instar is an especially vulnerable one. During the pupal life the insect has no means of offence, and having exceedingly limited powers of motion, it has almost no means of defense unless an armor has been provided.

Many larvæ merely retreat to some secluded place in which the pupal stadium is passed; others bury themselves in the ground; and still others make provision for this helpless period by spinning a silken armor about their bodies. Such an armor is termed a *cocoon*.

The cocoon is made by the full-grown larva; and this usually takes place only a short time before the beginning of the pupal stadium. But in some cases several months elapse between the spinning of the cocoon and the change to pupa, the cocoon being made in the autumn and the change to pupa taking place in the spring. Of course a greater or less portion of this period is occupied by the prepupal stadium.

Cocoons are usually made of silk, which is spun from glands already described. In some cases, as in the cocoons of *Bombyx*, the silk can be unwound and utilized by man.

While silk is the chief material used in the making of cocoons, it is by no means the only material. Many wood-boring larvæ make cocoons largely of chips. Many insects that undergo their transformation in the ground incorporate earth in the walls of their cocoons. And hairy caterpillars use silk merely as a warp to hold together a woof of hair, the hairs of the larva being the most conspicuous element in the cocoon.

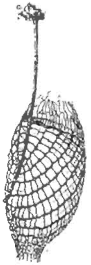

Fig. 210.—Lace-like cocoon of *Trichostibas parvula*, from which the adult has emerged.

In those cases in which silk alone is used there is a great variation in the nature of the silk, and in the density of the cocoon. The well-known cocoons of the saturniids illustrate one extreme in density, the cocoons of certain Hymenoptera, the other.

The fiberous nature of the cocoon is usually obvious; but the cocoons of saw-flies appear parchment-like, and the cocoons of the sphecids appear like a delicate foil.

While in the more common type of cocoons the wall is a closely woven sheet, there are cocoons that are lace-like in texture (Fig. 210).

Modes of escape from the cocoon.—The insect, having walled itself in with a firm layer of silk, is forced to meet the problem of a means of escape from this inclosure; a problem which is solved in greatly varied ways.

In many insects in which the adult has biting mouth parts, the adult merely gnaws its way out by means of its mandibles. In some cases, as the Cynipidæ, it is said that this is the only use made of its mandibles by the adult.

In some cases the mandibles with which the cocoon is pierced pertain to the pupal instar, this is true of *Chrysopa* and *Hemerobius;* and the Trichoptera break out from their cases, by means of their mandibles, while yet in the pupal state.

For those insects in which the adult has sucking mouth parts, the problem is even more difficult. Here it has been met in several quite distinct ways. The pupæ of many Lepidoptera possess a specialized organ for breaking through the cocoon; in some the anterior end of the pupa is furnished with a toothed crest (*Lithocolletes hamadryella);* in certain saturniids there is a pair of large, stout, black spines, one on each side of the thorax, at the base of the fore wings with which the pupa cuts a slit in the cocoon through which the adult emerges, this was observed by Packard in *Tropæa luna;* but as these spines are present in other saturniids, where the cocoon is too dense to be cut by them, and where an opening is made in some other way, it is probable that, as a rule, their function is locomotive, aiding the pupa to work its way out from the cocoon, by a wriggling motion.

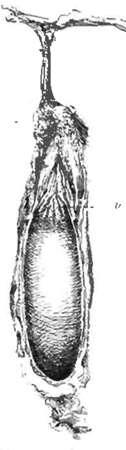

Fig. 211.—Longitudinal section of a cocoon of *Callosamia promethea; v*, valve-like arrangement for the escape of the adult.

Fig. 212.—Cocoon of *Megalopyge opercularis.*

Fig. 213.—Old cocoon of *Megalopyge opercularis.*

One of the ways in which saturniids pierce their cocoons is that practiced by *Bombyx* and *Telea.* These insects soften one end of the cocoon by a liquid, which issues from the mouth; and then, by forcing the threads apart or by breaking them, make an opening.

Far more wonderful than any of the methods of emergence from the cocoon described above are those in which the larva makes provision for the escape of the adult. The most familiar of these is that practiced by the larvæ of *Samia cecropia* and *Callosamia promethea*. These larvæ when they spin their cocoons construct at one end a conical valve-like arrangement, which allows the adult to emerge without the necessity of making a hole through the cocoon (Fig. 211, *v*). A less familiar example, but one that is fully as wonderful, is that of a *Megalopyge*. The larva of this species makes a cocoon of the form shown in Figure 212. After an outer layer of the cocoon has been made, the larva constructs, near one end of it, a hinged partition; this serves as a trap door, through which the moth emerges. That part of the cocoon that is outside of the partition is quite delicate and is easily destroyed. Hence most specimens of the cocoons in collections present the appearance represented in Figure 213.

The puparium.—The pupal stadium of most Diptera is passed within the last larval skin, which is not broken till the adult fly is ready to emerge. In this case the larval skin, which becomes hard and brown, and which serves as a cocoon, is termed a *puparium*. In some families the puparium retains the form of the larva; in others the body of the larva shortens, assuming a more or less barrel-shaped form, before the change to a pupa takes place (Fig. 214).

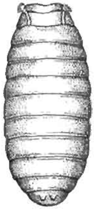

Fig. 214.—Puparium of *Trypeta*.

Modes of escape from the puparium.—The pupæ of the more generalized Diptera escape from the puparium through a T-shaped opening, which is formed by a lengthwise split on the back near the head end and a crosswise split at the front end of this (Fig. 215), or rarely, through a cross-wise split between the seventh and eighth abdominal segments. In the more specialized Diptera there is developed a large bladder-like organ, which is pushed out from the front of the head, through what is known as the frontal suture, and by which the head end of the puparium is forced off. This organ is known as the *ptilinum*. After the adult escapes, the ptilinum is withdrawn into the head.

The Different types of pupæ.—Three types of pupæ are commonly recognized; these are the following:

Fig. 215.—Puparium of a stratiomyiid.

Exarate pupæ.—Pupæ which, like those of the Coleoptera and Hymenoptera, have the legs and wings free, are termed exarate pupæ.

Obtected pupæ.—Pupæ which like the pupæ of Lepidoptera, have the limbs glued to the surface of the body, are termed obtected pupæ.

Coarctate Pupæ.—Pupæ that are enclosed within the hardened larval skin, as is the case with the pupæ of most of the Diptera, are termed coarctate pupæ.

The imago—The fully developed or adult insect is termed the *imago.*

The life of the imago is devoted to making provision for the perpetuation of the species. It is during the imaginal stadium that the sexes pair, and the females lay their eggs. With many species this is done very soon after the last ecdysis; but with others the egg-laying is continued over a long period; this is especially true with females of the social Hymenoptera.

h. HYPERMETAMORPHOSIS

There are certain insects, representatives of several different orders that exhibit the remarkable peculiarity in their development that the successive larval instars represent different types of larvæ. Such insects are said to undergo a hypermetamorphosis.

The transformations of several of these insects will be described later in the accounts of the families to which they belong; and for this reason, in order to avoid repetition, are not discussed here. The more striking examples are *Mantispa, Meloe, Stylops,* and *Platygaster.*

i. VIVIPAROUS INSECTS

There are many insects that produce either nymphs or larvæ instead of laying eggs. Such insects are termed *viviparous.* This term is opposed to *oviparous*, which is applied to those insects that lay eggs that hatch after exclusion from the body.

It has been pointed out in the discussion of the reproductive organs that, from the primordial germ-cells, there are developed in one sex spermatoza and in the other eggs; and it should be borne in mind that the germ-cells produced in the ovary of a female from the primordial germ-cells are eggs. These eggs grow and mature; in some cases they become covered with a shell, in others they are not so covered; in some cases they are fertilized by the union of a spermatozoan with them, and in others they are never fertilized; but in all these cases they are eggs. We may say, therefore, that all insects are developed from eggs.

A failure to recognize this fact has introduced confusion into entomological literature. Some writers have termed the germ-cells produced by agamic aphids *pseudova* or false eggs. But these germ-cells are as truly eggs as are those from which the males of the honeybee develop; they are merely unfertilized eggs. The term pseudovum conveys a false impression; while the phrase, an unfertilized egg, clearly states a fact.

Some writers make use of the term ovoviviparous indicating the production of eggs that have a well-developed shell or covering, but which hatch within the body of the parent; but the distinction is not fundamental, since viviparous animals also produce eggs as indicated above.

Among viviparous insects there are found every gradation from those in which the larvæ are born when very young to those in which the entire larval life is passed within the body of the parent. There also exist examples of viviparous larvæ, viviparous pupæ, and viviparous adults. And still another distinction can be made; in some viviparous insects the reproduction is parthenogenetic; in others it is sexual.

Viviparity with parthenogenetic reproduction.—In certain viviparous insects the reproduction is parthenogenetic; that is, the young are produced from eggs that are not fertilized. This type of reproduction occurs in larvæ, pupæ, and apparently in adults.

Pædogenetic Larvæ.—In 1862 Nicholas Wagner made the remarkable discovery that certain larvæ belonging to the Cecidomyiidæ give birth to living young. This discovery has been confirmed by other observers, and for this type of reproduction the term *pædogenesis*, proposed by Von Baer, has come into general use. This term is also spelled *pedogenesis*; the word is from *pædo* or *pedo*, a child, and *genesis*.

The phenomenon of pædogenesis is discussed later in the accounts of the Cecidomyiidæ and of the Micromalthidæ.

Pædogenetic pupæ.—The most frequently observed examples of pædogenetic reproduction are by larvæ; but that pupæ also are sometimes capable of reproduction is shown by the fact that Grimm ('70) found that eggs laid by a pupa of *Chironomus grimmii*, and of course not fertilized, hatched.

Anton Schneider ('85) found that the adults of this same species of *Chironomus* reproduced parthenogenetically. This species, therefore, exhibits a transition from pædogenesis to normal parthenogenesis.

Viviparous adult agamic females.—There may be classed under this class provisionally, the agamic females of the Aphididæ; as these are commonly regarded as adults. It has been suggested, however, that the agamic reproduction of the Aphids may be a kind of pædogenesis; the agamic females being looked upon as nymphs. This however, is not so evident in the case of the winged agamic generation. On the other hand, the reproductive organs of the agamic aphids are incompletely developed, as compared with those of the sexual forms, lacking a spermatheca and colleterial glands.

This discussion illustrates the difficulty of attempting to make sharp distinctions, whereas in nature all gradations exist between different types of structure and of development. Thus Leydig ('67) found a certain aphid to be both oviparous and vivaprous; the eggs and the individuals born as nymphs being produced from neighboring tubes of the same ovary.

Viviparity with sexual reproduction.—Although most insects that reproduce sexually are oviparous, there are a considerable number in which sexual reproduction is associated with viviparity.

Among these sexual viviparous insects there exist great differences in method of reproduction; with some the young are born in a very immature stage of development, a stage corresponding to that in which the young of oviparous insects emerge from the egg; while with others the young attain an advanced stage of development within the body of the mother.

Sexual viviparous insects giving birth to nymphs or larvæ.—That type of viviparity in which sexual females give birth to very immature nymphs or larvæ exists in more or less isolated members of widely separated groups of insects. As the assumption of this type of reproduction involves no change in the structure of the parent, but merely a precocious hatching of the egg, it is not strange that it has arisen sporadically and many times. In some cases, however, the change is not so slight as the foregoing statement would imply; as, for example, in the case of the viviparous cockroach, which does not secrete oothecæ as do other cockroaches.

Among the recorded examples of this type of viviparity are representatives of the Ephemerida, Orthoptera, Hemiptera, Lepidoptera, Coleoptera, Strepsiptera, and Diptera.

Sexual viviparous insects giving birth to old larvæ.—The mode of reproduction exhibited by these insects is doubtless the most exceptional that occurs in the Hexapoda, involving, as it does, very important changes in the structure of the reproductive organs of the females.

With these insects the larvæ reach maturity within the body of the parent, undergoing what is analogous to an intra-uterine development, and are born as full-grown larvæ. This involves the secretion of a "milk" for the nourishment of the young.

This mode of reproduction is characteristic of a group of flies, including several families, and known as the Pupipara. This name was suggested for this group by the old belief that the young are born as pupæ; but it has been found that the change to pupa does not take place till after the birth of the larva.

The reproduction of the sheep-tick, *Melophagus ovinus*, may be taken as an illustration of this type of development; this is described in the discussion of the Hippoboscidæ, the family to which this insect belongs.

The giving birth to old larvæ is not restricted to the Pupipara. Surgeon Bruce (quoted by Sharp, '99) has shown that the Tse-tse-fly, *Glossina morsitans*, reproduces in this way, the young changing to pupæ immediately after birth.

An intermediate type of development is illustrated by *Hylemyia strigosa*, a dung-frequenting fly belonging to the Anthomyiidæ. This insect, according to Sharp ('99), produces living larvæ, one at a time. "These larvæ are so large that it would be supposed they are full-grown, but this is not the case, they are really only in the first stage, an unusual amount of growth being accomplished in this stadium."

j. NEOTEINIA

The persistence with adult animals of larval characteristics has been termed *neoteinia** or *neotenia*. When this term first came into use it was applied to certain amphibians, as the axolotle, which retains its gills after becoming sexually mature; but it is now used also in entomology.

The most familiar examples of neoteinic insects are the glow-worms, which are the adult females of certain beetles, the complemental females of Termites, and the females of the Strepsiptera.

II. THE DEVELOPMENT OF APPENDAGES

In the preceding pages the more obvious of the changes in the external form of the body during the metamorphosis of insects and some deviations from the more common types of development have been discussed. The changes in the form of the trunk that have been described are those that can be seen without dissection; but it is impracticable to limit a discussion of the development of the appendages of the body in this way, for in the more specialized types of metamorphosis a considerable part of the development of the appendages takes place within the body-wall.

*Neoteinia: neos (νέος), youthful; teinein (τείνειν), to stretch.

a. THE DEVELOPMENT OF WINGS

Two quite distinct methods of development of wings exist in insects; by one method, the wings are developed as outward projecting appendages of the body; by the other, they reach an advanced stage of development within the body. The former method of development takes place with nymphs and naiads, the latter with larvæ.*

1. *The Development of the Wings of Nymphs and Naiads*

In insects with a gradual or with an incomplete metamorphosis the development of the appendages proceeds in a direct manner. The wings of nymphs and naiads are sac-like outgrowths of the body-wall, which appear comparatively early in life and become larger and larger with successive molts, the expanding of the wing-buds taking place immediately after the molt; an illustration of this has been given in the discussion of gradual metamorphosis, page 175.

2. *Development of the Wings in Insects with a Complete Metamorphosis*

Although there are differences in details in the development of the wings in the different insects undergoing a complete metamorphosis, the essential features are the same in all. The most striking feature is that the rudiments of the wings, the wing-buds, arise within the body and become exposed for the first time when the last larval skin is shed. The development of the wings of the cabbage butterfly (*Pontia rapæ*) will serve as an example of this type of development of wings. The tracing of that part of this development which takes place during the larval life can be observed by making sections of the body-wall of the wing-bearing segments of the successive instars of this insect.

The first indication of a wing-bud is a thickening of the hypodermis; this thickening, known as a *histoblast* or an *imaginal disc*, has been observed in the embryos of certain insects, in the first larval instar of the cabbage butterfly it is quite prominent (Fig. 216, *a*). During the second stadium, it becomes more prominent and is invaginated, forming a pocket-like structure (Fig. 216, *b*). During the third stadium a part of this invagination becomes thickened and evaginated into the pocket formed by the thinner

*Only the more general features of the development of wings are discussed here. For a fuller account see "The Wings of Insects" (Comstock '18, *a*).

portions of the invagination (Fig. 216, *c*). During the fourth stadium, the evaginated part of the histoblast becomes greatly extended (Fig. 216, *d*). It is this evaginated portion of the histoblast that later becomes the wing. During the fifth stadium the wing-bud attains the form shown in Figure 216, *e*, which represents it dissected out of the wing-pocket At the close of the last larval stadium, the fifth, the wing is pushed out from the wing-pocket, and lies under the old larval cuticula during the prepupal stadium. It is then of the form shown in Figure 216, *f*. The molt that marks the beginning of the pupal stadium, exposes the wing-buds, which in the Lepidoptera become closely soldered to the sides and breast of the pupa. Immediately after the last molt when the adult emerges, the wings expand greatly and assume their definitive form.

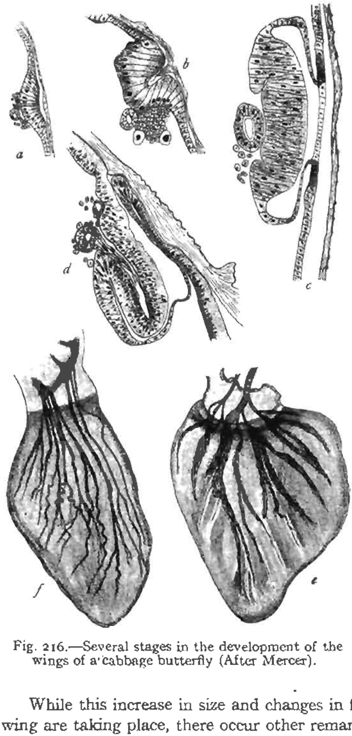

Fig. 216.—Several stages in the development of the wings of a cabbage butterfly (After Mercer).

While this increase in size and changes in form of the developing wing are taking place, there occur other remarkable developments in its structure. *A connection is made with a large trachea near which* the histoblast is developed, shown in cross-section in the first four

parts (*a*, *b*, *c*, and *d*) of Figure 216; temporary respiratory organs, consisting of bundles of tracheoles, are developed (*e* and *f*); and later, near the close of the larval period, the tracheæ of the wing are developed, and the bundles of tracheoles disappear. During the later stages in the development of the wing the basement membranes of the hypodermis of the upper and lower sides of the wing come together, except along the lines where the veins are to be developed later, and become united. In this way the wing is transformed from a bag-like organ to a sheet-like one. The lines along which the two sides of the wing remain separate are the vein cavities; in these the trunks of the wing-tracheæ extend. During the final stages of the development of the wing, the walls of the vein-cavities are thickened, thus the wing-veins are formed; and the spaces between the wing-veins become thin.

By reference to Figure 216, *c* and *d*, it will be seen that the histoblast consists of two quite distinct parts, a greatly thickened portion which is the wing-bud and a thinner portion which connects the wing-bud with the hypodermis of the body-wall, and which constitutes the neck of the sac-like histoblast, this is termed the *peripodal membrane*, a term suggested by the similar part of the histoblast of a leg; and the enclosed cavity is known as the *peripodal cavity*.

In the more specialized Diptera, the peripodal membranes are very long and both the wing-buds and the leg-buds are far removed from the body-wall. A condition intermediate between that which exists in the Lepidoptera, as shown in Figure 216, and that of the more specialized Diptera was found by Kellogg ('07) in the larva of *Holorusia rubiginosa*, one of the crane-flies (Fig. 217).

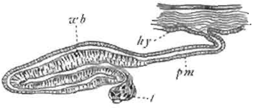

Fig. 217.—Wing-bud in the larva of the giant crane-fly, *Holorusia rubiginosa*; *hy*, hypodermis; *pm*, peripodal membrane; *t*, trachea; *wb*, wing-bud (After Kellogg).

b. THE DEVELOPMENT OF LEGS

The development of the legs proceeds in widely different ways in different insects. In the more generalized forms, the legs of the embryo reach an advanced stage of development before the nymph or naiad leaves the egg-shell, and are functional when the insect is born; on the other hand, in those specialized insects that have vermiform larvæ, the development of the legs is retarded, and these organs do not become functional until the adult stage is reached. Almost every conceivable intergrade between these two extremes exist.

1. The Development of the Legs of Nymphs and of Naiads

In insects with a gradual metamorphosis and also in those with an incomplete metamorphosis the nymph or naiad when it emerges from the eggshell has well-developed legs, which resemble quite closely those of the adult. The changes that take place in the form of the legs during the postembyronic development are comparatively slight; there may be changes in the relative sizes of the different parts; and in some cases there is an increase in the number of the segments of the tarsus; but the changes are not sufficiently great to require a description of them here.

2. The Development of the Legs in Insects with a Complete Metamorphosis

It is a characteristic of most larvæ that the development of their legs is retarded to a greater or less extent. This retardation is least in campodeiform larvæ, more marked in eruciform larvæ, and reaches its extreme in vermiform larvæ.

The development of the legs of insects with campodeiform larvæ.—Among the larvæ classed as campodeiform the legs are more or less like those of the adults of the same species; there may be differences in the proportions of the different segments of the leg, in the number of the tarsal segments, and in the number and form of the tarsal claws; but these differences are not of a nature to warrant a discussion of them here. These larvæ lead an active life, like that of nymphs, and consequently the form of legs has not been greatly modified from the paurometabolous type.

The development of the legs of insects with eruciform larvæ.—In caterpillars and other eruciform larvæ the thoracic legs are short and fitted for creeping; this mode of locomotion being best suited to their mode of life, either in burrows or clinging to foliage. This form of leg is evidently an acquired one being, like the internal development of wings, the result of those adaptive changes that fit these larvæ to lead a very different life from that of the adults.

In the case of caterpillars the thoracic legs are short, they taper greatly, and each consists of only three segments. It has been commonly believed and often stated that the three segments of the larval leg correspond to the terminal portion of the adult leg; but studies of the development of the legs of adults have shown that the divisions of the larval leg have no relation to the five divisions of the adult leg.

It has been shown by Gonin ('92), Kellogg ('01 and '04), and Verson ('04) that histoblasts which are the rudiments of the legs of the adult exist within the body-wall of the caterpillar at the base of the larval legs. Late in the larval life the extremity of the legs of the adult are contained in the legs of the caterpillar. It has been shown that the cutting off of a leg of a caterpillar at this time results in a mutilation of the terminal part of the leg of the adult.

The development of the legs of the adult within the body of caterpillars has not been studied as thoroughly as has been the development of the wings; but enough is known to show that in some respects the two are quite similar; this is especially true of the development of the tracheoles and of the tracheæ.

The development of the legs in insects with vermiform larvæ.—In vermiform larvæ the development of the entire leg is retarded. The leg arises as a histoblast, which is within the body and bears, in its more general features, a resemblance to the wing-buds of the same insect. The development of the legs of vermiform larvæ has been studied most carefully in the larvæ of Diptera. During the larval life the leg becomes quite fully developed within the peripodal cavity; in *Corethra*, they are spirally coiled; in *Musca*, the different segments telescope into each other. At the close of the larval period, the evagination of the legs takes place.

c. THE DEVELOPMENT OF ANTENNÆ

1. The Transformation of the Antennæ of Nymphs and of Naiads

In the case of nymphs and of naiads the insect when it emerges from the eggshell has well-developed antennæ. The changes that take place during the postembryonic development are, as a rule, comparatively slight; in most insects, an increase in the number of the segments of the antennæ takes place; but in the Ephemerida, a reduction in number of the antennal segments occurs.

2. The Development of the Antennæ in Insects with a Complete Metamorphosis

One of the marked characteristics of larvæ is the reduced condition of the antennæ; even in the campodeiform larvæ of the Neuroptera, where the legs are comparatively well-developed, the antennæ are greatly reduced.

In eruciform larvæ the development of the antennæ follows a course quite similar to that of the legs. The larval antennæ are small;

the antennæ of the adult are developed from histoblasts within the head and during the latter part of the larval life are folded like the bellows of a closed accordian; at the close of this period they become evaginated, but the definitive form is not assumed until the emergence of the adult. A similar course of development of the antennæ takes place in vermiform larvæ (Fig. 218).

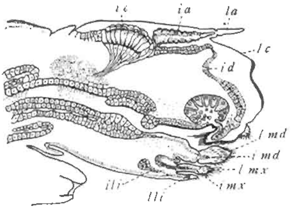

Fig. 218.—Sagittal section through head of old larva of *Simulium*, showing forming imaginal head parts within. *lc*, larval cuticula; *id*, imaginal head-wall; *la*, larval antenna; *ia*, imaginal antenna; *ie*, imaginal eye; *lmd*, larval mandible; *imd*, imaginal mandible; *lmx*, larval maxilla; *imx*, imaginal maxilla; *lli*, larval labium; *ili*, imaginal labium (From Kellogg).

d. THE DEVELOPMENT OF THE MOUTH-PARTS

Great differences exist among insects with reference to the comparative structure of their mouth-parts in their immature and adult instars. In some insects the immature instars have essentially the same type of mouth-parts as the adults; in most of these cases, the mouth-parts are of the biting types, but in the Homoptera and Heteroptera both nymphs and adults have them fitted for sucking; in many other insects, the mouth-parts of the larvæ are fitted for biting while those of adults are fitted for sucking; and in still others, as certain maggots, the development of the mouth-parts is so retarded that they are first functional in the adult insect. Correlated with these differences are differences in the method of development of these organs.

In those insects that have a gradual or incomplete metamorphosis and in the Neuroptera, the Coleoptera, and the Hymenoptera in part, the mouth-parts of the immature and adult instars are essentially of the same type. In these insects the mouth-parts of each instar are developed within the corresponding mouth-parts of the preceding instar. At each ecdysis there is a molting of the old cuticula, a stretching of the new one before it is hardened, a result of the growth in size of the appendages, and sometimes an increase in the number of the segments of the appendage. In a word, the mouth-parts of the adult are developed from those of the immature instar in a comparatively direct manner. In some cases, however, where the mouth-

parts of the larva are small and those of the adult are large, only the tips of the developing adult organs are within those of the larva at the close of the larval period, a considerable part of the adult organs being embedded in the head of the old larva.

In a few Coleoptera and Neuroptera (the Dytiscidæ, Myrmeleonidæ, and Hemerobiidæ) the larvæ, although mandibulate, have the mouth-parts fitted for sucking. In these cases the form of the mouth-parts have been modified to fit them for a peculiar method of taking nourishment during the larval life. The mouth-parts of the adults are of the form characteristic of the orders to which these insects belong.

In those insects in which the larvæ have biting mouth-parts and the adults those fitted for sucking, the development is less direct. In the Lepidoptera, for example, to take an extreme case, there are great differences in the development of the different organs; within the mandibles of the old larvæ there are no developing mandibles, these organs being atrophied in the adult; but at the base of each larval maxilla, there is a very large, invaginated histoblast, the developing maxilla of the adult; these histoblasts become evaginated at the close of the larval period, but the maxillæ do not assume their definitive form till after the last ecdysis.

The extreme modification of the more usual course of development of the mouth-parts is found in the footless and headless larvæ of the more specialized Diptera. Here the mouth-parts do not appear externally until during the pupal stadium and become functional only when the adult condition is reached. See the figures illustrating the development of the head in the Muscidæ (Fig. 220).

It should be noted that the *oral hooks* possessed by the larvæ of the more specialized Diptera are secondarily developed organs and not mouth-parts in the sense in which this term is commonly used. These oral hooks serve as organs of fixation in the larvæ of the Œstridæ and as rasping organs in other larvæ.

e. THE DEVELOPMENT OF THE GENITAL APPENDAGES

The development of the genital appendages of insects has been studied comparatively little and the results obtained by the different investigators are not entirely in accord; it is too early therefore to do more than to make a few general statements.

In the nymphs of insects with a gradual metamorphosis rudimentary genital appendages are more or less prominent and their develop-

ment follows a course quite similar to that of the other appendages of the body.

In insects with a complete metamorphosis the genital appendages are represented in the larvæ by invaginated histoblasts; the develop-ing appendages become evaginated in the transformation to the pupa state and assume their definitive form after the last ecdysis.

III THE DEVELOPMENT OF THE HEAD IN THE MUSCIDÆ

In the more generalized Diptera the head of the larva becomes, with more or less change, the head of the adult; the more important of these changes pertain to the perfecting of the organs of sight and the development of the appendages, the antennæ and mouth-parts.

But in the more specialized Diptera there is an anomalous retarding of the development of the head, which is so great that the larvæ of these insects are commonly referred to as being acephalous. This retarded development of the head has been carefully studied by Weisman ('64), Van Rees ('88) and Kowalevsky ('87). The accompanying diagrams (Fig. 220) based on those given by the last two authors illustrate the development of the head in *Musca*, which will serve as an illustration of this type of development of the head.

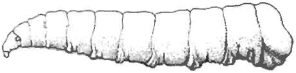

Fig. 219.—Larva of the house-fly, *Musca domestica* (After Hewitt).

The larvæ of *Musca* are conical (Fig. 219); and the head-region is represented externally only by the minute apical segment of the conical body. It will be shown later that this segment is the neck of the insect, the developing head being invaginated within this and the following segments. This invagination of the head takes place during the later embryonic stages.

In Figure 220 are given diagrams, adapted from Kowalevsky and Van Rees, representing three stages in the development of the head of *Musca*. Diagram A represents the cephalic end of the body of a larva; and diagram B and C, the corresponding region in a young and in an old pupa respectively; the parts are lettered uniformly in the three diagrams.

The three thoracic segments (1, 2, and 3) can be identified by the rudiments of the legs (l^1, l^2, and l^3). In the larva (A) the leg-buds are far within the body, the peripodal membrane being connected with

the hypodermis of the body-wall by a slender stalk-like portion. In the young pupa (B) the peripodal membranes of the histoblasts of the legs are greatly shortened and the leg-buds are near the surface of the body; and in the old pupa (C) the leg-buds are evaginated. The wing-buds are omitted in all of the diagrams.

In the first two segments of the body of the larva (A) there is a cavity (*ph*) which has been termed the "pharynx"; this is the part in which the oral hooks characteristic of the larvæ of the Muscidæ develop. The name pharynx is unfortunate as this is not a part of the alimentary canal; it is an invaginated section of the head, into the base of which the œsophagus (*æ*) now opens.

In the figure of the larva (A) note the following parts: the œsophagus (*æ*); the ventral chain of ganglia (*vg*), the brain (*b*), and a

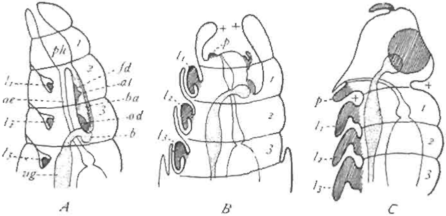

Fig. 220.—Development of the head in the Muscidæ. A, larva; B, young pupa; C, old pupa (From Korschelt and Heider after Kowalevsky and Van Rees).

sac (*ba*) extending from the so-called pharynx to the brain. There are two of these sacs, one applied to each half of the brain, but only one of these would appear in such a section as is represented by the diagram. These sacs were termed the *brain-appendages* by Weismann. In each of the "brain-appendages" there is a disc-like thickening near the brain, the *optic disc* (*od*); this is a histoblast which develops into a compound eye; in front of the optic disc there is another prominent histoblast; the *frontal disc* (*fd*), upon which the rudiment of an antenna (*at*) is developed.

In the larva the brain and a considerable part of the "brain-appendages" lie within the third thoracic segment. In the young pupa (B) these parts have moved forward a considerable distance; and in the old pupa (C) the head has become completely evaginated. The part marked *p* in the two diagrams of the pupa is the rudiment of the proboscis.

By comparing diagrams B and C it will be seen that what was the tip of the first segment of the larva and of the young pupa (++) becomes the neck of the insect after the head is evaginated.

IV. THE TRANSFORMATIONS OF THE INTERNAL ORGANS

Great as are the changes in the external form of the body during the life of insects with a complete metamorphosis, even greater changes take place in the internal organs of some of them.

In the space that can be devoted to this subject in this work, only the more general features of the transformation of the internal organs can be discussed; there is an extensive and constantly increasing literature on this subject which is available for those who wish to study it more thoroughly.

In insects with a gradual or with an incomplete metamorphosis there is a continuous transformation of the internal organs, the changes in form taking place gradually; being quite comparable to the gradual development of the external organs; but in insects with a complete metamorphosis, where the manner of life of the larva and the adult are very different, extensive changes take place during the pupal stadium. The life of a butterfly, for example, is very different from that it led as a caterpillar; the organs of the larva are not fitted to perform the functions of the adult; there is consequently a necessity for the reconstruction of certain of them; hence the need of a pupal stadium. Pupæ are often referred to as being quiet; but physiologically the pupal period is the most active one in the post-embryonic life of the insect.

In those cases where a very marked change takes place in the structure of internal organs, there is a degeneration and dissolution of tissue, this breaking down of tissues is termed *histŏlysis*.

In the course of histolysis some cells, which are frequently leucocytes or white blood corpuscles, feed upon the debris of the disintegrating tissue; such a cell is termed a *phăgocyte*, and the process is termed *phăgocytōsis*. It is believed that the products of the digestion of disintegrating tissue by the phagocytes pass by diffusion into the surrounding blood and serve to nourish new tissue.

After an organ has been more or less broken down by histolysis, the extent of the disintegration differing greatly in different organs and in different insects, there follows a growth of new tissue; this process is termed *histogĕnesis*.

The histogenetic reproduction of a tissue begins in the differentiation and multiplication of small groups of cells, which were not affected by the histolysis of the old tissue; such a group of cells is termed an *imaginal disc* or a *histoblast*. They were termed imaginal discs on account of the disc-like form of those that were first described and because they are rudiments of organs that do not become functional till the imago stage; but the term histoblast is of more general application and is to be preferred.

The extent of the transformation of the internal organs differs greatly in different insects. In the Coleoptera, the Lepidoptera, the Hymenoptera, and the Diptera Nemocera, the mid-intestine and some other larval organs are greatly modified, but there is no general histolysis. On the other hand, in the Diptera Brachycera, there is a general histolysis. In *Musca* all organs break down and are reformed except the central nervous system, the heart, the reproductive organs, and three pairs of thoracic muscles. Regarding the extent of the transformations in the other orders where the metamorphosis is complete we have, as yet, but little data.

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